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UNDERSTANDING AND MISUNDERSTANDING THE MIGRATION OF THE MONARCH BUTTERFLY (NYMPHALIDAE) IN NORTH AMERICA: 1857–1995

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ABSTRACT. Since 1857, amateurs and professionals have woven a rich tapestry of biological information about the monarch butterfly's migration in North America. Huge fall migrations were first noted in the midwestern states, and then eastward to the Atlantic coast. Plowing of the prairies together with clearing of the eastern forests promoted the growth of the milkweed, *Asclepias syriaca,* and probably extended the center of breeding from the prairie states into the Great Lakes region.

Discovery of overwintering sites along the California coast in 1881 and the failure to find consistent overwintering areas in the east confused everyone for nearly a century. Where did the millions of monarchs migrating southward east of the Rocky Mountains spend the winter before their spring remigration back in to the eastern United States and southern Canada? Through most of the 20th century, the Gulf coast was assumed to be the wintering area, but recent studies rule this out because adults lack sufficient freezing resistance to survive the recurrent severe frosts.

Seizing the initiative after C. B. Williams' (1930) review of monarch migration, Fred and Norah Urquhart developed a program that gained the interest of legions of naturalists who tagged and released thousands of monarchs to trace their migration. Just as doubts in the early 1970s over whether there really were overwintering aggregations of the eastern population, on 2 January 1975 two Urquhart collaborators, Kenneth and Cathy Brugger, discovered millions of monarchs overwintering high in the volcanic mountains of central Mexico. This allowed a synthesis of the biology of this remarkable insect, including its migration and overwintering behaviors, its spread across the Pacific Ocean to Australia, its coevolution with milkweeds, and its elaborate milkweed-derived chemical defense which probably makes possible the dense aggregations during the fall migration and at the overwintering sites.

Many important questions remain. Can monarchs migrate across the Gulf of Mexico? Can they migrate at night? Do they exploit strong tailwinds? Do they migrate to Central America? Do they overwinter elsewhere in Mexico or Central America? How much interchange is there between the eastern and western North American populations? How important is the fall migration along the Atlantic coast compared to the migration west of the Appalachian Mountains? What causes annual fluctuations in the size of the fall migrations?

Beautiful and mysterious, the monarch's overwintering colonies in Mexico rank as one of the great biological wonders of the world. Unfortunately, these colonies are the monarch's Achilles' heel because of human population growth and deforestation in the tiny Oyamel fir forest enclaves. Additional risks arise from the increasing use of herbicides across North America which kill both larval and adult food resources. As a result, the migratory and overwintering biology of the eastern population of the monarch butterfly has become an *endangered biological phenomenon.* Without immediate implementation of effective conservation measures in Mexico, the eastern migration phenomenon may soon become biological history.

In writing this paper for Charles Remington's honorarial issue of the *Journal of the Lepidopterists' Society,* fond memories flood forth of my days as his graduate student at Yale University from 1953 to 1957. My very first seminar lecture was on the migration of the monarch butterfly, *Danaus plexippus* (L.), and this set the stage for what will soon be 40 years of studying diverse aspects of the biology of this fascinating creature (reviews in Brower 1977a, 1984, 1985a, 1985b, 1986, 1987b, 1988, 1992).

The present paper reconstructs the history of understanding the migration of the monarch butterfly in North America. To my knowledge, a detailed analysis of the ideas and the people who developed them has never been attempted. The story, a result of the combined observations of professional and amateur lepidopterists over more than a century, reflects the spirit in which Charles Remington, then a graduate student at Harvard, and his friend and colleague Harry Clench founded The Lepidopterists' Society in 1947 (Clench 1977). My purpose is to weave together the strands, to follow some of the red herrings, and to discuss several aspects of the migration biology that are still incompletely understood. Timely resolution of these questions should enhance efforts to preserve the monarch's mass migratory and overwintering behaviors which, regrettably, have become an endangered biological phenomenon (Brower & Pyle 1980, Brower & Malcolm 1989, 1991).

The first great student of the monarch butterfly was Charles Valentine Riley, who emigrated from England and rose to lead midwestern, and then national entomology in the USA (Packard 1896, Essig 1931). In addition to being a first rate scientist, Riley was a talented artist who beautifully illustrated his descriptions of insect natural histories, and he fostered the English tradition of collating and publishing letters from a diversity of field observers, including many on the migration of the monarch. Anecdotal science on the monarch predominated well into the 20th century. In 1930, C. B. Williams of Edinburgh University reviewed monarch migration in his book, *The Migration of Butterflies*, which he periodically updated (Williams 1938, 1958, Williams et al. 1942). Shortly after the founding of The Lepidopterists' Society, Williams (1949:18) called for information from members and defined questions for much of the migration research that would follow: "What happens to the butterflies that fly through Texas in the fall? Do they go on to Mexico? If so, do they hibernate there, or remain active, or breed?"

University of Toronto entomologist Fred A. Urquhart and his wife Norah took up the Williams challenge in 1940 and began tracing the fall migration of the monarch via a long-term tagging program, which would come to involve more than 3,000 research associates (Urquhart 1941, 1952, 1960, 1978, 1979, 1987, Anon. 1955). The Urquharts communicated with their collaborators through an annual newsletter, published numerous papers on monarch biology, and carried on the tradition of incorporating amateurs' notes in their writings. According to Urquhart and Urquhart (1994), the final newsletter to their Insect Migration Association was issued as Volume 33 in 1994.

Speculations about the destination of the eastern monarch migration became increasingly confused throughout the first three quarters of the 20th century because of the mysterious disappearance of what had to be vast numbers of butterflies that annually bred over an area of at least three million square kilometers. Many tortuous hypotheses were devised until resolution came in Urquhart's August 1976 *National Geographic* article announcing the discovery of the phenomenal overwintering aggregations in Mexico. This culmination of the Urquharts' lifetime efforts was one of the great events in the history of lepidopterology.

FIRST OBSERVATIONS OF THE FALL MIGRATION: REPORTS FROM KANSAS TO CONNECTICUT

Aside from a possible sighting of monarchs migrating in eastern Mexico during one of Christopher Columbus's expeditions (Doubleday & Westwood 1846–1852:91), D'Urban (1857) was apparently the first to report a migration of monarch butterflies. He described the butterflies appearing in the Mississippi Valley in "such vast numbers as to darken the air by the clouds of them" (p. 349). During September 1867 in southwestern Iowa, Allen (in Scudder & Allen 1869) described monarchs gathered in several groves of trees bordering the prairie "in such vast numbers, on the lee sides of trees, and particularly on the lower branches, as almost to hide the foliage, and give to the trees their own peculiar color" (p. 331). Although this clustering behavior was initially interpreted as a means of avoiding strong prairie winds, it soon became evident that it was associated with large southward movements of monarchs in the fall.

The first collated evidence of massive fall migrations was published in 1868 by two American entomologists, Benjamin Dann Walsh and Charles Valentine Riley, who had independently emigrated from England to Illinois and were both keen to establish entomology as a science useful to farmers. Additionally, as evidenced in Darwin's correspondence (in F. Darwin and Seward 1903a:248–251, 1903b:385–386), Walsh and Riley were both influenced by *The Origin of Species* (Darwin 1859). Walsh, born in 1808, developed his interest in insects when he was nearly 50 years old, and launched his career in 1865 as associate editor of the *Practical Entomologist* in which he wrote, reprinted and edited numerous articles and letters, and answered letters from curious people and farmers besieged by insect pests. Within a decade he became the first Illinois State Entomologist (Riley 1870, Darwin and Seward 1903a). In contrast, Riley, born in 1843, had left his family home in England at the age of 17. By the time he was 20, he had begun publishing entomological notes in the Chicago-based *Prairie Farmer* (Ashmead 1895) and shortly thereafter became the journal's prolific entomological editor. In September 1868 the two men founded *The American Entomologist*, which Riley continued after Walsh died prematurely in

1869 (Riley 1870). In 1868 Riley was appointed State Entomologist of Missouri, in 1876 he moved to Washington, D.C. to become Chief of the newly founded U.S. Entomological Commission, and shortly thereafter he founded the Smithsonian Institution's insect collections.

Beginning in 1864, Riley used the *Prairie Farmer* to establish a correspondence network with midwestern farmers who were plagued by the migratory Rocky Mountain Locust. Combining his observations and high quality drawings with the information in hundreds of letters from farmers and lay people, Riley generated enormous interest in insect life histories in both the United States and Canada. He also published prolifically in virtually all the major biological journals of the period: Derksen and Scheiding-Göllner (1968) listed 50 pages of Riley's references. Among his many achievements was rescuing the French wine industry by unraveling the life history of the grape *Phylloxera* (Phylloxeridae) which had 19 distinct forms (Riley 1874, Smith 1992). In what may be considered the founding paper on the broad study of the biology of the monarch, Riley (1871) described and illustrated the life histories and mimicry of the monarch and viceroy butterflies. Darwin wrote Riley on 1 June 1871 saying "I am struck with admiration at your powers of observation. . . . The discussion on mimetic insects seems to me particularly good and original" (in Darwin & Seward 1903b:386).

As pointed out by Dr. Edward Smith, (letter to LPB, 10 June 1994), the garnering of information on monarch movements and numbers was a valuable outcome of the network of farmers that Riley had set up. Correspondents indicated that monarchs appeared in great abundance in several midwestern states during September 1868. Thus in Riley (1868) and in Walsh and Riley (1868), Davis described the sudden appearance of vast swarms in different parts of Madison, Wisconsin; Barnard noted great multitudes in Manteno, Illinois; and Sibley recounted millions flying over St. Joseph, Missouri. Peabody (1880) independently recalled having seen another large swarm in Racine, Wisconsin in the first week of September, 1868 (Racine is on the western shore of Lake Michigan south of Milwaukee). Westcott (1880) reported large flights and clustering in Racine during September or October in two of the seven years between 1873–1880. Although Bethune (1869) noted monarchs as abundant in the Toronto area in July 1869, no swarms were reported that year. During September and October 1870, Wells (in Riley 1871) noted large numbers of monarchs flying overhead in a S/SW direction through both Manhattan, Kansas and Alton, Illinois.

New reports during the 1870s extended the range of the fall swarming behavior farther east. Monarchs were exceedingly common during the summer of 1871 throughout New England (Sprague 1871), and in September, Saunders (1871:157) observed "vast numbers—I might safely say millions" clustering on a semicircle of trees on the Canadian shore of Lake Erie, about 130 km NNE of Cleveland, Ohio. This was the first report that associated overnight roosting with the swarming behavior. Werneburg (in Scudder 1889:1083) had also noted endless masses migrating southwesterly through Connecticut in 1871. The following fall (1872) an immense swarm was observed in flight over Cleveland, Ohio, where the butterflies remained abundant for several days (Ison, in Riley et al. 1875). Ison speculated that the monarchs had flown across Lake Erie from Canada. He was undoubtedly correct because Point Pelee, Ontario, to the northwest of Cleveland, was later determined to be a major concentration point for the fall migration across Lake Erie (Moffat 1901b, Saverner 1908).

ESTABLISHING THE MONARCH AS A BIRD-LIKE MIGRANT

In relating numerous accounts of the monarch congregating in "immense swarms or bevies" in the prairie states, Riley (1871:151) struggled to understand the significance of this annual "assembling" behavior. As was then in vogue in the entomological community (cf. Hall 1887), Riley considered insect movements as largely irruptive, and initially eschewed the idea that the monarch butterfly could perform directed long distance flights comparable to the migration of birds. He tentatively hypothesized (p. 152) that during "the seasons when the milkweeds are either destroyed [i.e. in the fall] or have not yet started to grow [i.e. in the early spring] . . . low temperatures of the seasons instinctively prompt them to wend their way southwards. The probabilities are that these swarms are eventually destroyed". . . Re-establishment of monarchs the following spring in the north, therefore, had to depend on the survival of hibernating "impregnated females" that begin laying their eggs early in May. Riley thus initially propounded an emigration-death hypothesis for the "migrating bevies" and assumed that the re-establishment of the monarch populations the following spring was by the breeding of the non-migrant individuals which had successfully hibernated through the winter in the north.

In August 1875, Riley, Saunders, Scudder and others exchanged ideas on the swarming behavior at a sub-meeting of the Cambridge Entomological Club held in Chicago (Anon. 1875). William Saunders, the preeminent Canadian entomologist of his time, founded the Entomological Society of Ontario and later, along with Charles Bethune, would found the influential *Canadian Entomologist*. Samuel H. Scudder (1889) published *The Butterflies of the Eastern United States and Canada with Special Reference to New England* and became one of the most famous 19th century U.S. butterfly biologists (for further biographical information, see Bethune 1909, Essig 1931, Clench 1947, Remington 1947 and Mallis 1971). While the word "migration" is conspicuously absent from the proceedings, this 1875 meeting was historically significant because it instigated an international interest in monarch travels.

In early October 1876, William H. Edwards (1877) observed a line of butterflies flying southward continuously for an hour near Boston (Edwards, another prominent 19th century lepidopterist, is best known for his beautiful *The Butterflies of North America*, 1868–1897). On reading the October report, Scudder (1877) speculated that the butterflies must have been monarchs, and interpreted the observation as migration per se. Both Edwards and Scudder subsequently maintained a long-term interest in the monarch and were frequently at odds over interpreting the most current data.

The accumulation of anecdotal notes of monarch swarms from the prairie across the Great Lake States to New England, supplemented by frequent newspaper and signal officer reports of swarms passing over Iowa, Kansas, Missouri, and Texas, finally convinced Riley (1878a:273–274, republished in 1878b) that the monarch indeed performs a bird-like fall migration. While still maintaining that a few individuals hibernate in the north, he now proposed that, following the deterioration of milkweeds, most of the monarchs instinctively congregate in masses and migrate southward to find nectar sources and "to reach a warmer country in which to hibernate." With great prescience, he contended that "Southerly timber regions offer most favorable conditions for such hibernation" (pp. 273–274).

Stroop's (in Stroop & Riley 1870, see also Riley 1871:151) springtime observation of a "bevy" of about 30 worn monarchs south of Dallas, Texas on 31 March 1870 appears to have been a key piece of the puzzle: Riley now (1878a:274) proposed that the few females that survived hibernation "upon waking from their winter torpor, make at once for the prairies, where the milkweeds most abound. Faded and often tattered, they may be seen flying swiftly over such prairies. . . I have no doubt but that they travel thus for many hundreds of miles, keeping principally to the north, and, ere they perish, supplying the milkweeds here and there with eggs. . . . In short, these migrations find their readiest explanation in the instinct of the species to lengthen the breeding season and to extend its range. . . . There is a southward migration late in the growing season in congregated masses [i.e. a fall migration], and a northward dispersion [i.e. a spring remigration] early in the season through isolated individuals."

The next piece of the puzzle bore out Riley's (1878a, 1878b) hunch about where monarchs must spend the winter. Roland Thaxter (1880, republished in 1881), who would become a professor of botany at Harvard University (Clark 1941), in January 1873 observed huge numbers of monarchs densely aggregated across an acre of pine trees along the Gulf Coast in Apalachicola, Florida, about 100 km southwest of

Tallahassee. Riley (1880b) seized upon Thaxter's discovery as proving that the bird-like migration of the monarch involved a fall migration to the south, hibernation there during the winter months, and a return migration the following spring. However, he still maintained that most of the hibernating individuals comprising the overwintering swarms must perish. In what may have been his final view on overwintering, Riley (in Riley et al. 1893:270) published an observation of monarchs having been eaten by mice along the Gulf Coast in Texas, while "hidden away in their hibernating quarters in the south."

Riley's increasingly sophisticated understanding of monarch biology was cut short on 14 September 1895, when he died at the age of 52 as a result of a bicycle accident (Remington 1947a, Mallis 1971). It was indeed ironic that, 25 years before his own accidental death, Riley (1870) had described the loss of his co-editor and mentor Benjamin Walsh, who died from internal injuries sustained while jumping out of the way of a locomotive in his hometown in Rock Island, Illinois.

TUTT'S CHALLENGE AND MOFFAT'S REBUTTAL

By the end of the 19th century, J. W. Tutt, editor of the British *Entomologist's Record and Journal of Variation*, was drawn into the fray, thus initiating overseas interest in monarch migration. Tutt (1898, 1899, 1900) rejected Riley's two-way migration hypothesis and held that the monarch was no different from the known one-way migrants (=emigrants) such as *Vanessa atalanta* (L.) (Nymphalidae) or *Colias croceus* Geoffroy (Pieridae), which breed continuously in their native habitats in southern Europe and north Africa. Periodically over-reproducing there, they emigrate to England where they produce one or more generations, which then die during the winter without a return migration (cf. Carter & Hargreaves 1986).

Tutt (1902:262–263) finally argued that the purported fall migration of monarchs had been misinterpreted; rather, he maintained that they were dispersing at random in the fall, perishing without overwintering and without hibernating. Recolonization of the north would periodically occur when the monarchs, analogous to *Vanessa* and *Colias*, again over-bred in their southern range and spread northward, breeding through the summer on the milkweeds, and then all dying (see also Tutt 1900: 185, 208, 254).

Tutt's challenge was summarily rejected by Scudder (1898) and then rebutted by John Alston Moffat (1901b), an amateur entomologist who was secretary of the Entomological Society of Ontario (Bethune 1905). Moffat's prior papers on the monarch (1880–1900) had been largely observational, but he now combined facts and hypotheses in a thoughtful review of the literature. In his words, the monarch "is a southern butterfly, which has inherited a powerful migratory instinct, and is endowed with a capacity to indulge it to the utmost limit. . . . The northern portion of the American Continent . . . is where it finds the conditions most favorable for . . . multiplying . . . to an unlimited extent. But it cannot endure frost, therefore goes southerly in autumn, and . . . gathers in immense swarms before it starts out. It makes the journey in easy stages, spending months on the way. As it does not hibernate, it keeps on the move south-west until its breeding season comes around, when these, or more southerly bred specimens, start the northerly movement" (Moffat 1901b:50).

Moffat (1902b) urged Thaxter to fill in the details of the behavior of the butterflies he had seen overwintering along the Florida Gulf Coast in the winter of 1873. Thaxter (in Moffat 1902b) replied that the butterflies had begun to scatter and mate in February. This now fully convinced Moffat that monarchs were not hibernating per se along the Gulf Coast, but were passing the winter in an active but reproductively repressed state. Moffat deduced that a northward spring remigration of these monarchs in February would be too early for them to exploit the spring milkweed resurgence in the north. He then proposed a new, complex hypothesis: the Florida butterflies must fly farther southward in search of milkweeds, while those that had flown even farther south in the fall would fly northward, also in search of milkweeds.

Lugger (in Riley et al. 1890) noted that numerous monarchs migrating through Baltimore in October had frozen. Moffat had reviewed freezing resistance in insects (1893), and with considerable insight, he was dubious that Florida and the Gulf Coast could be successful overwintering areas. He had noted an adult monarch that froze to death on his windowsill (1901a) and mentioned (1901b) having seen dead chrysalids after frosts. Citing occasional northern cold fronts which had been reported to destroy orange groves and even to have killed overwintering bluebirds in Florida, he (1902b) proposed that such frosts would kill all the overwintering monarchs along the south Atlantic states. Noting that the northern region had been recolonized successfully by monarchs but not by bluebirds after a big freeze, Moffat astutely reasoned that the recolonizing monarchs must have originated, not from Florida, but from their "tropical home" (p. 81). Thus, while not explicitly stating it, Moffat proposed a frost-free winter breeding range for the monarch south of the continental United States which would be the source of the spring remigrants. This would have to be Mexico, the Caribbean, Central America or South America. As far as I can ascertain, he has never been credited for this important deduction, probably because Tutt (1902: 292–295) regarded the collective evidence as inadequate.

EARLY SPECULATIONS AND OBSERVATIONS ON THE FALL MIGRATION TO MEXICO

The first suggestion that monarchs migrate to Mexico per se apparently was made by Jennie Brooks (1907, 1911), a naturalist who for several years had observed them migrating through Lawrence, Kansas during the autumn. In her words, "From the north they came . . . to the south they swept away . . . as far as I could see them—to Texas, to Louisiana, to Mexico" (1907:111), and "all along the Canada line east and west the mighty winged host of monarchs advances, when instinct stirs, straight down across the states to Mexico" (1911:48). Brooks' 1907 essay also was the first detailed description of the monarch's clustering behavior during the fall migration. She combined elegant prose, high quality observation, counts of monarchs in the clusters, and actual experimental manipulation. No one before or since has so fully documented watching the quiescent monarchs all night long, their reaction to the rising sun, cluster break-up, and resumption of the southward migration. Her 1911 essay, published in the beautiful magazine *Country Life in America*, included the very first photograph—taken by flashlight—of "sleeping monarchs on the twigs of a cedar tree." In an article adjacent to Brooks', Thoms (1911) provided further quantitative data: during August 1910 at Green Lake, Minnesota, one cluster contained 300 individuals, another 500. His note included a photograph of disturbed monarchs flying against the sky in which he counted 1,300 individuals.

There are remarkably few records of the fall migration through Mexico (Urquhart 1960:261–262). The first was made in 1890 by Sir Rider Haggard (in Williams et al. 1942:171) who reported thousands of monarchs flying southward in Orizaba, an area east of Mexico City along the easternmost peak of the Transverse Neovolcanic Belt. The most substantive observation was Rzedowski's (1957) on 27–28 October 1956 along the Sierra Madre Oriental, near Ciudad del Maiz in the State of San Luis Potosi at about 1100–1500 m elevation. He and an assistant saw small numbers of monarchs flying over the vegetation through a xeric habitat 2–6 m above the ground in a sustained southeasterly direction. Later in the afternoon, they also observed the formation of an aggregation: hundreds of monarchs zeroed in and vied for position (=assembling behavior) on one of several mesquite trees (*Prosopis juliflora* D.C., Leguminosae). Speculating on the southeasterly direction of the migration, Rzedowski offered two hypotheses: the monarchs were following the southeasterly trajectory of the Sierra Madre Oriental, or they were actively crossing these mountains to reach the humid tropical regions along eastern Mexico (I interpret Rzedowski's comments as implying that the monarchs were either headed (a) to an unknown overwintering area, or (b) to a lowland area where they could breed). In the same paper, Rzedowski also reported that Pelaz had observed a migration through the same area in December 1951. The southeasterly direction of the migration through this area subsequently was verified by Calvert in the late 1970s (unpublished observations, summary in Calvert & Brower 1986).

The apparent absence of representations of monarch butterflies in the art and pottery of prehispanic Mexico (Beutelspacher 1980, 1988) is curious, but may be related to the fact that the principal overwintering area was in a "no man's land" between the Aztec culture to the east and the Tarascan culture to the west (Arbingast et al. 1975:24, 73). It could be profitable to search the early Mexican literature in more detail for records on the overwintering and migrations, e.g., the late 18th century writings of botanist-explorer Don Martin de Sesé and the renaissance Mexican, José Antonio Alzate, who reported on many scientific and natural history topics (see Motten 1950, Leopold 1959).

Monarchs migrate in great numbers through Angangueo in northeastern Michoacan (Brower & Calvert, personal observations 1977–1995). This town is near the center of the major overwintering areas, including the Sierra Campanario, Sierra Chincua, Sierra Chivati and Sierra Pelon (see Fig. 1 in Calvert & Brower 1986). In 1909 Angangueo's rich silver mines came under the control of the American Smelting and Refining Corporation (ASARCO), part of the Guggenheim family empire (Carreño 1983). More than 3,000 workers shipped 200 tons of high grade silver ore every day to the ASARCO smelters in Aguascalientes (Bernstein 1964:56, O'Connor 1932). In their quest for riches, apparently no one ever took the time to record the incredible numbers of migrants swirling around them on the way to overwintering valleys, less than 15 km from the center of town.

YEARS OF MUDDLING: THE HIBERNATION HYPOTHESIS

Nineteenth century lepidopterists knew that several species of Holarctic nymphalid butterflies in the genera *Gonepteryx, Nymphalis, Polygonia,* and *Vanessa* survive winter freezing in the north temperate region as adults inside of tree holes and hollow logs, and this they called "hibernation" (see Holland 1898, Ford 1945, Urquhart 1978, Young 1980, Scott, 1986). Riley had described hibernating larvae in Nymphalid butterflies, including *Limenitis archippus* (Cramer) (1871) and *Asterocampa* (Riley 1874), and apparently assumed (1871:144) that "impregnated" monarch females can survive the winter in the north by hibernating in the adult stage. The facts that trickled in did little to settle the issue. For example, in Amherst, Massachusetts, Parker (1872: 115) reported "an interesting capture of a much worn and faded female *Archippus*" on 12 May 1871 . . . as "bearing on the winter history of the species" (nineteenth century monarch nomenclature varied, and included the generic names *Anosia, Danais* and *Danaus*, and the specific names *archippus, menippe* and *plexippus*; see Scudder 1889:726, Ackery & Vane Wright 1984:202.)

The hibernation hypothesis had been accepted uncritically by Saunders (1873), Scudder and Gulick (1875), Edwards (1876a, 1876b, 1878), Weir (1876), Distant (1877) and Bowles (1880). Riley (1878b:273–274) firmly restated that "The *archippus* butterfly hibernates." However he now rejected "Saskatchewan country" as a place of hibernation, implying that they would freeze to death in the far north. He still maintained that they hibernated in "the temperate belt . . . within hollow trees and in other sheltered situations," and he speculated that the major hibernation range would prove to be in "the southerly timbered regions." Thaxter's (1880) discovery of overwintering butterflies along the Florida Gulf Coast led Riley (1880b:101) to place even more emphasis on the south as the place of hibernation, and Riley was now dubious about the prairies where "there is a want of protecting forest as will permit hibernation . . . even if the butterflies could withstand the severe winter" (see also Riley et al. 1890). Scudder (1889:727–748) struggled with the evidence for and against hibernation in the north, and appears to have concluded that a few do survive winters as adults, at least as far north as New England. This view subsequently prevailed in his popular book *Frail Children of the Air* (1895:141) as indicated by his statement that "woodsmen sometimes, in cleaving open a tree, will discover a little colony of hibernating butterflies, as has been done in the case of the monarch."

Moffat (1888) doubted that monarchs quiescently hibernate inside trees. He had observed that the first individuals appeared in Ontario in late May, and, noting their wing wear, deduced that they were too fresh to have hibernated. Further doubt was generated by Emily Morton (1888:226–227) in lower New York state. "Having been requested by my friend, Mr. Wm. H. Edwards, to make observations on *Danais Archippus*," Morton reported that she had peeled and split "many and many a stump" in search of hibernating monarchs, without success. She did, however, discover a mourning cloak (*Nymphalis antiopa* (L.) Nymphalidae) "torpid, though still alive . . . in the very center of a stump cosily mixed up with the damp saw-dust left by the ants and other borers." Holland (1898:82), in the first edition of his popular and influential *The Butterfly Book* (see Remington 1947b), apparently accepted Moffat's deduction, stating that monarchs do not hibernate in "any stage of their existence." Moffat (1901b:49), reflecting on Thaxter's observation that monarchs were copulating during their sojourn along the Gulf Coast of Florida, concluded that "we have not the slightest reason to believe that they hybernate (sic) at all, anywhere."

Moffat (1902b:79), now intent on rejecting the hibernation hypothesis, asked Thaxter to provide the exact dates of his observations. Thaxter replied that he had first sketched the clustering butterflies on 3 January 1873 and that the swarms did not begin to scatter until February, at which time many were seen "*in coitu*" (these dates had been confirmed by Scudder 1889:743, who also had written to Thaxter). Armed with this supplemental evidence, Moffat concluded that the flocks of monarchs "were not there in search of a place to hibernate, but with the intention of passing the time in an active state until their season of breeding had arrived" (p. 79). He confidently entitled this paper: "*Anosia archippus* does not hibernate."

Early workers recognized that courtship, oviposition and egg maturation were repressed in monarchs immediately prior to the fall migration (Edwards 1878, Riley 1878b, Moffat 1901b). However, they lacked sufficient knowledge to associate these changes with the day-length and hormonally mediated syndrome (Johnson 1969, Barker & Herman 1976b) that we now know controls several aspects of monarch physiology and behavior. These include the onset and breaking of reproductive diapause, the associated repression and stimulation of sexual activity, the fall and spring migrations, and the aggregations along the fall migratory routes and at the overwintering sites (Brower 1985a, Rankin et al. 1986, Scoble 1992, Herman 1993, James 1993, McNeil et al. 1995).

Moffat's ultimate rejection of hibernating in the north was embraced by the lepidopterists' community well into the 20th century (e.g., Ricker 1906, Inkersley 1911, Shannon 1916, Comstock 1927, Shepardson 1939: 26, Holland 1940, 1945:101, Shannon 1954). However, Williams' (1930: 152–153) seminal review of butterfly migration apparently ignored the rejection because of the discovery of quiescent overwintering colonies of monarchs in California (see below). This clearly indicated that monarch adults do hibernate in some parts of their annual range, as Riley had realized (Riley & Bush 1882). Failure to locate consistent overwintering areas east of the Rockies, together with the deductive rather than empirical evidence against hibernation adduced by Moffat, led several authors (e.g., Clark 1941:534, Klots 1951, Baker 1978, Shull 1987) to speculate that monarch adults and perhaps even pupae can withstand freezing temperatures. They thus ressurected the idea that monarchs hibernate in the north!

In retrospect, Riley's intellectual intermingling of the physiological phenomenon of hibernation with the geographic location of hibernation proved a major distraction in understanding the migration of the monarch (Ackery & Vane-Wright 1984). The discovery of monarchs overwintering in Mexico, together with our modern understanding of insect diapause, would seem to provide the necessary coup de grâce to the recurrent hypothesis that monarchs hibernate in their summer breeding range.

DID THE MIGRATION EXPAND EASTWARDS DURING THE LATTER PART OF THE 19TH CENTURY?

Prior to the 1880s, as we have seen, the majority of reports of fall "swarming behavior" were from the Great Plains states. Riley (1880b: 101) had described monarchs flourishing on "the vast plains and prairies lying to the north between the Mississippi River and the Rocky Mountains" where "milk-weeds abound." While this may have reflected his living in the midwest as Missouri State Entomologist, it also is possible that the Great Plains were where most monarch breeding did naturally occur. Perhaps significantly, Doubleday and Westwood (1846–1852:90) stated that "*Danais Archippus*" is abundant even in "the largest towns of the Middle and Northern states." Shannon's (1916:229–230) description of monarchs migrating through Minnesota, Iowa, Kansas, Oklahoma and eastern Texas is certainly consistent with the early observations. Contrasting these numbers with the smaller migrations through Illinois and the states to the east, he stated that the "wide highways of the Great Plains and West Central States offer the most frequent reports of remarkable butterfly spectacles . . . gatherings of almost unbelievable magnitude . . . move forward in . . . congregations . . . miles in width . . . forming veritable crimson clouds."

I feel it is significant that it was not until the 1880s that large fall migrations and aggregations were reported farther east and along the Atlantic coast. Abbott (1887:80) described a migration of monarchs extending 40 km in length through New Jersey in September 1881 and stated that "several such migrations occurred at about this time in the New England and Middle States." Wintle (1885:179–180) noted large numbers of clustering monarchs in the Montreal area on 22 August 1885 and said "I don't remember having seen this species so abundant here for several years" (whether they were as abundant at an earlier date is implied, but moot). The build-up throughout the east must have been widespread in 1885, because Hamilton (1885) recounted accumulations along the New Jersey coast during the first week of September as "almost past belief . . . millions is but feebly expressive . . . miles of them is no exaggeration." Ellzey's (1888) report on the 23 September 1886 migration through southern Maryland along the Chesapeake Bay was equally vivid: "The whole heavens were swarming with butterflies . . . an innumerable multitude of them." Another large migration was reported (Anon. 1896) along the Atlantic Coast over Ocean City, Maryland on 13 September 1896: a northeasterly wind was blowing and the "heavens became almost black with swarms of huge red-winged butterflies" moving in a southerly direction for at least an hour.

I propose that Riley's emphasis on the prairie states as the original center of summer breeding was not biased and that monarchs actually expanded their area of intensive breeding from the midwestern to the eastern states during the latter part of the 19th century. This would have been caused by plowing and deforestation greatly altering milkweed distributions and abundances in both the prairie and the northern forest ecosystems (Marks 1983). Plowing virtually destroyed the 433 million acres of the original midwestern prairie (Sims 1988) which was host to about 22 habitat-specific and non-weedy *Asclepias* species (Rydberg 1932, Woodson 1954, Wilbur 1976, Barkley 1977). Even Minnesota, one of the northernmost prairie states, has 16 milkweed species, several of which were abundant (Upham 1884). With the introduction of the John Deere steel plow in 1837 and the twenty mule combine harvesters by the 1880s, diminution of the native prairie flora proceeded at an astonishing rate (Weaver 1954, Vankat 1979, Petulla 1988). Heavy grazing by cattle and sheep began in the 1860s and by 1910 most of the grasslands had been plowed and replaced with grain fields (McAndrews 1988). The extent of ruination of this magnificent native North American environment is staggering: for example, less than 0.5% of Missouri's original 15 million prairie acres (Robbins & Esterla 1992) and less than 1% of Wisconsin's 2 million prairie acres are still intact (Curtis 1959). The resultant changes in relative abundance of the various herbaceous species would have dramatically altered not only the monarchs' larval menu, but also the nectar bonanza provided by the rich diversity of the Compositae and other herbaceous plants amongst the original prairie grasses (see Conrad 1952:66, Risser et al. 1981).

Ironically, while milkweed habitat was drastically altered in the midwest, newly habitable areas were being generated in the northeast. By 1860 most of the northeastern deciduous forest had been cut, and between 1860 and 1890, 50 million more acres of forest were cleared across the Great Lake region (Cronin 1983, Williams 1989). As Urquhart and Urquhart pointed out (1979:41–42), there is little doubt that clearing the forest vastly increased the abundance of a single species of milkweed, *Asclepias syriaca* L. Thus, Haley (1887:80) had reported the monarch as beneficial in Brownfield, Maine because "Its foodplant (*Asclepias*) is very troublesome to farmers," and Scudder (1888:66) implied that milkweeds had become extremely abundant in hayfields. Seitz (1924:113) stated that the monarch accompanies "cultivation further and further into the primeval forest as soon as a few clearings have been formed where foodplants of the larvae, species of *Asclepias,* can get a foothold." This spread of *A. syriaca* into the opened forest areas was consistent with the fact that it is the one truly weedy species of the 29 native milkweeds in the monarch's summer breeding range east of the Rocky Mountains (Whiting 1943, Woodson 1954:28).

The combined destruction of the prairie flora and the opening of the eastern forest thus caused an increase in the abundance of *Asclepias syriaca* that undoubtedly caused monarchs to expand their summer breeding from the Grass Land Province into the Eastern Deciduous Forest Province, as delineated in Gleason and Cronquist (1964:174, Fig. 1). This Eastern Deciduous Forest Province is virtually congruent with the distribution of *Asclepias syriaca* and with the summer breeding area currently considered most important for monarchs (Urquhart 1960: 66, 298, Urquhart & Urquhart 1976b:80, 1980:722). Whether a net increase in milkweed biomass in eastern North America resulted from these changes—as opposed to a shift onto the geographically expanded *A. syriaca* resource—is an important question that may be unanswerable (see "Columbus hypothesis" below).

We have confirmed the overwhelming predominance of *A. syriaca* as the current foodplant of the fall generation of monarchs of the eastern North American population by means of cardiac glycoside fingerprinting. This is a chemical technique developed by James Seiber, Carolyn (Roeske) Nelson, and me in the 1970s (Roeske et al. 1976, Brower et al. 1982, reviewed in Brower 1984). It utilizes the fact that monarch larvae ingest toxic chemicals called cardiac glycosides (also known as cardenolides) from milkweed plants that they eat in the wild. We showed that many species of North American milkweeds have different arrays of these poisons, and that the specific array sequestered by larvae feeding on different milkweed species remains intact through to the adult stage. By extracting the poisons from individual butterflies and visualizing the poison array on a thin layer chromatography plate, we can determine a specific "cardiac glycoside fingerprint" for each wild captured monarch. Adults originating from different geographic regions, that have eaten different species of milkweeds, consequently have different cardiac glycoside fingerprints. The technique has limitations: some milkweed species have similar arrays of poisons and some have none or very low concentrations of them. However, we were able to determine that more than 90% of 386 monarchs collected at the overwintering sites in Mexico had fed on *A. syriaca*, and thus quantitatively confirmed the Urquharts' hypothesis (Seiber et al. 1986, Malcolm et al. 1989, Malcolm et al. 1993, Table 5).

So far, monarchs have been recorded feeding on only 27 of the known 108 North American *Asclepias* species (Ackery & Vane-Wright 1984, Malcolm and Brower 1986). These 27 species include 12 that are native to the Great Plains (Barkley 1977). However, I predict that most, if not all, *Asclepias* species (as well as several Asclepiadaceous species in other native milkweed genera; Ackery & Vane-Wright 1984:202) will eventually prove to be monarch foodplants in the wild. If it were possible to locate an intact collection of monarchs made in the midwest between 1860–1880, the butterflies could be fingerprinted and compared to monarchs reared on the native *Asclepias* species of the area. This would permit a test of the hypothesis that the butterflies switched from a diverse milkweed menu largely to *A. syriaca* as the prairies were plowed and the forests cut.

MIGRATION OF THE WESTERN POPULATION

Jennie Bush (in Riley & Bush 1881, 1882) reported three Monterey pines (*Pinus insignus* Dougl. =*P. radiata*, Pinaceae) completely covered with monarchs in Monterey, California on 27 February 1881. She also stated that "A lady resident informed me that for the 12 years she had lived there the appearance had been the same" i.e., back to 1869 (1881: 572). Kellog (1904) noted similar behavior on Point Pinos in nearby Pacific Grove, also on the Monterey Peninsula. Citing the rarity of milkweeds within 50 miles of the Monterey area, his own observations of extensive breeding 80 km to the north, and his knowledge of the eastern migration, Kellog was the first person to infer that monarchs also migrate in California. Inkersly (1911:283) provided the first detailed description of monarchs overwintering in Pacific Grove, and speculated that they probably originated in "the country west of the Rocky Mountains."

Three years later Lucia Shepardson (1914) published a remarkable pamphlet on the Pacific Grove monarchs. Although she cited no published reports, her writing indicates that she was aware of the then-current monarch literature. It is unfortunate that she has been largely ignored by subsequent monarch researchers because she had an impressive grasp of the larger picture of the monarch's "annual migration . . . phenomenon" (p. 12). As verbatim (p. 28, italicized parenthetical phrases added by LPB): "One of their most noted characteristics, mentioned by all authorities on butterflies, is their tendency at the end of summer to gather in great swarms, as if preparing for a long flight. At such times they are found clinging in masses upon low trees and shrubs *(aggregation behavior)*, just as they cling to the pines during their long sojourn *(the overwintering period)* in the Monterey woods, but as yet the latter place is the only known spot where they remain thus assembled for any length of time, their gatherings which have been observed elsewhere *(i.e., presumably the eastern population)* being only temporary, a day or two in duration at the longest." Her own observations indicated that the monarchs had returned *(migrated)* to the Pacific Grove trees back to 1898, and that the "earliest authentic information" (p. 12) dated their having been seen there back to 1864. Her revised edition (Shepardson 1939) provided an astonishing wealth of new information, including a wonderful description of the fall migration across the Monterey Bay from the Salinas and Santa Clara Valleys, bivouacking (i.e., late afternoon cluster formation), site fidelity, frost resistance (but see Teale 1956:343), rapid breakup of the colony in the spring, and annual variation in the numbers of overwintering butterflies.

Shepardson was the first person who clearly distinguished the eastern and western migratory populations of the monarch. She wrote: "It is presumed that those which are in the eastern and middle-western states go to the south during the cold weather, while those which winter near Pacific Grove come from a large part of the country lying west of the Rocky Mountains" (p. 29). She supported her implied fall migration hypothesis by citing observations made by forest rangers "every year" at the end of September in the Siskiyou Mountains of north central California. In her words "a long stream of them travels down through the hills from the north. . . . They fly a little below the tree tops, a thin and fluttering band about fifty feet wide . . . unwavering . . . they keep to an unerring course evidently with a fixed destination in view". . . This destination—the Pacific Grove butterfly trees—would constitute a southward journey of 725 km.

Shepardson's second-hand account of the southward flight through the Siskiyous was the first accepted documentation of a fall migration of the western population. Williams et al. (1942:167) appear to have unearthed the original observation, which had been made by Alan Forbes. "In August 1912, at Marble Mts., Siskiyou County . . . an observer at the summit of the pass, much lower than the surrounding mountains, suddenly came upon an amazing line of butterflies. They were coming up the slope as far as could be seen, then crossing the summit, and immediately descending . . . the flight was watched for half an hour and was . . . passing 'in countless millions' . . . 10 to 20 feet above the ground."

However, John Lane (pers. comm., 1994) has suggested that the butterflies may not have been monarchs because *Nymphalis californica* Bdv. (Nymphalidae) is known to have colossal migrations through this region (e.g., Whittaker 1953) and the two butterflies have somewhat similar color patterns. This possibility of confusion is lessened by additional observations. Mary Barber (1918:5–6), in another overlooked and informative booklet, *Winter Butterflies in Bolinas*, stated that Bolinas (immediately north of San Francisco) "is the winter home of the Monarch butterfly which comes not only from the Sierra Nevada mountains but also from the western ranges of the Rockies." In describing the fall migration, she wrote "Thousands of these frail butterflies start on their long journey toward the Pacific, in search of a mild climate, free from frost and snow, in which they can live all winter.

In Nevada County (California) great flocks of them have been seen, following the course of a stream downwards from the mountains towards the sea." These were unlikely to be *Nymphalis* because monarchs breed extensively along the forks of the Yuba and American Rivers that drain the western slope of the Sierra Nevadas in Nevada and Placer Counties (Brower et al. 1982, 1984b). Orr's (1970:91) description lends further credence to huge fall migrations in the Pacific states: "In Washington in 1928 a flock of monarchs estimated to be several miles wide and ten to fifteen miles long was observed in the Cascade Mountains. The number of individuals in this flock was believed to be in the billions."

In her revised edition, Shepardson (1939) added that the monarchs migrate into Pacific Grove from as far north as British Columbia, are seen in vast numbers each autumn in the Santa Cruz Mountains, and fly in from east of Pacific Grove, from the Santa Clara Valley and Santa Lucia Mountains, where they had bred. However, the absence of hard data on the routes of the fall migration in the West apparently led Essig (1926:639) simply to state that monarchs are "migratory in habits and their great numbers in many parts of Southern California during the winters are probably the result of a southern migration from the north Pacific states." Essig (in Williams 1930) later extended the geographic extent of the overwintering sites from Monterey to San Diego. I find it curious that Essig did not refer to the observations either of Ms. Shepardson or Ms. Baker.

More than 50 years after Downes reviewed the Pacific Coast data (in Williams et al. 1942:160), his conclusion is still true, that "the precise point of origin of the autumn migration, and the course of both the autumn and spring flights, seems largely to be unknown." Recent research by Lane (1984, 1985) and Nagano and Lane (1985) has documented at least 200 overwintering colonies along the Pacific Coast, from northern Baja California, Mexico to north of San Francisco, in Mendicino County (see also Nagano & Sakai 1988, Sakai et al. 1989, Sakai & Calvert 1991). As Wenner and Harris (1993) pointed out, however, the numerous winter aggregations in California imply but do not prove that there is a fall migration in the West comparable to that of the eastern population. Unfortunately, as Wenner and Harris also observed, the Urquharts' release and recapture data have never been published with sufficient detail to document the western fall migration unequivocally (Urquhart 1960:320, 1965a, Urquhart et al. 1970, Urquhart & Urquhart 1977a, Urquhart 1987:169 and Plate 12).

In contrast to the inadequacy of the data supporting the fall migration in the West, data obtained from tagging butterflies at the coastal overwintering sites in California definitely have established a long distance spring remigration eastwards across the Coast Range. Thus Urquhart

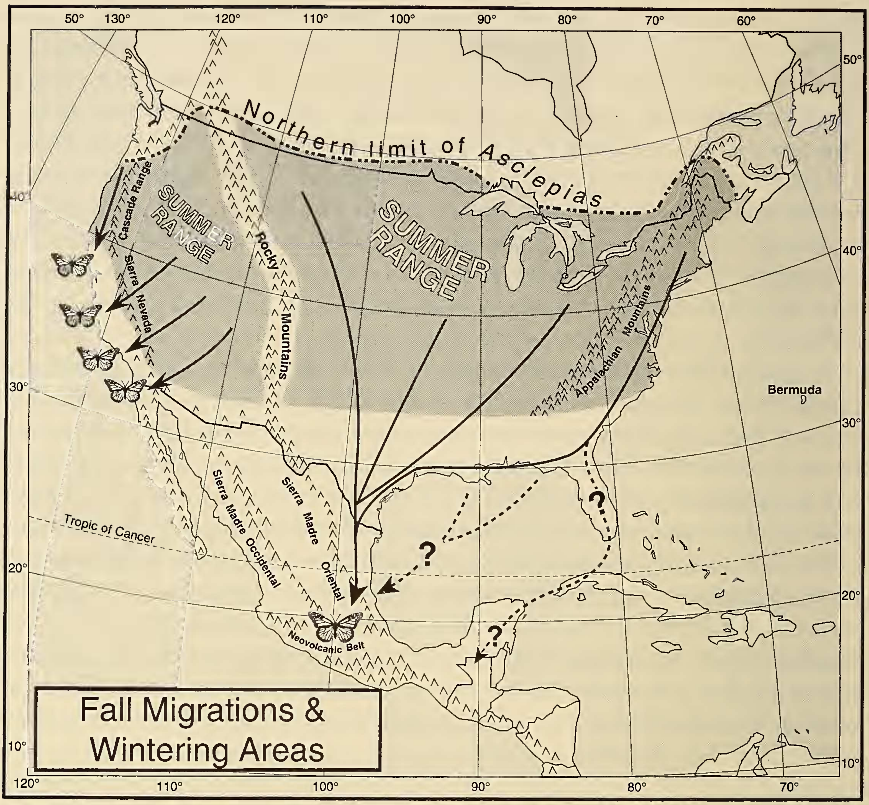

FIG. 1A. Fall migrations of the monarch butterfly in North America. Two migratory populations of the monarch occur in North America. The *western population* breeds west of the Rocky Mountains during the spring and summer and migrates to numerous overwintering sites, mainly along the California Coast, from north of San Francisco to south of Los Angeles. The second, much larger *eastern population* breeds east of the Rocky Mountains and migrates south to about twelve overwintering sites in the high peaks of the Transverse Neovolcanic Belt, south of the Tropic of Cancer in central Mexico. The last summer generation of monarchs in the East breeds principally on the abundant *Asclepias syriaca* milkweed which grows in an area of at least 2.6 million square km. The occasionally reported overwintering sites along the Gulf Coast are unstable because of periodic freezing, and migration across the Gulf of Mexico and Cuba remains hypothetical. The demarcation between the eastern and western populations is also hypothetical, and the degree of natural interchange between them is unknown, but probably minimal (revised, originally from Brower & Malcolm 1991).

(1960, Table 11) reported that 9 butterflies tagged at several overwintering sites near Monterey were recaptured in the Central Valley, and Beard (in Zahl 1963), who released more than 4,000 tagged monarchs in the same general area, reported 6 recaptures in the Sierra Nevada foothills. During 1985 and 1986, Nagano et al. (1993) marked 57,771 butterflies at 14 overwintering sites further south in California. The authors analyzed 100 recaptures that had flown from 10 to 465 km

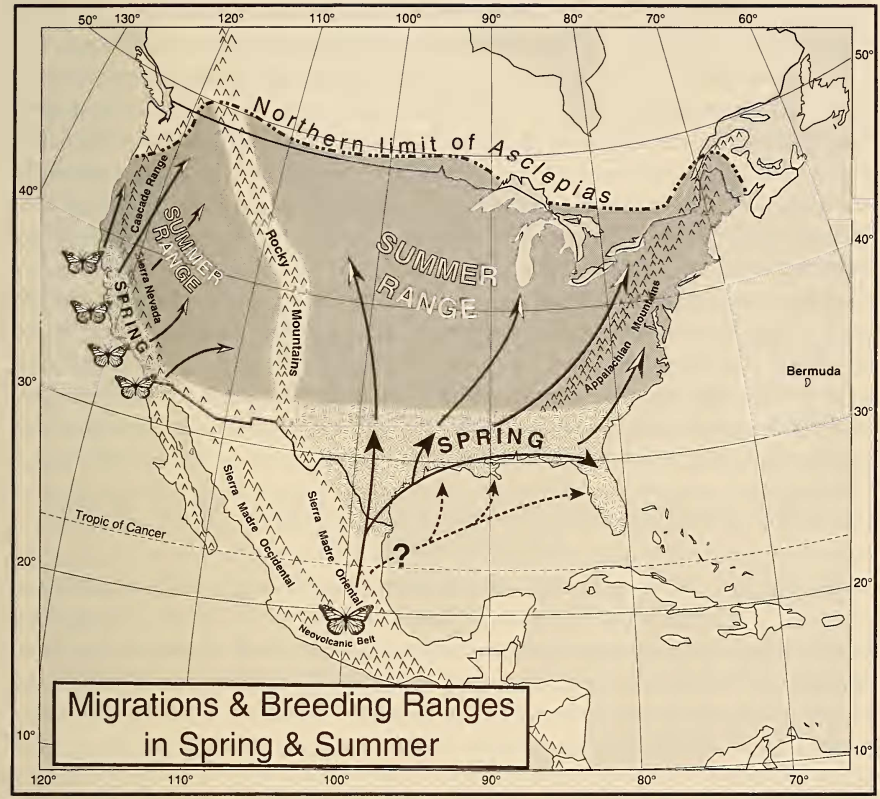

FIG. 1B. Spring remigrations of the monarch butterfly in North America. Overwintered individuals of the western population remigrate in early spring into the Coast Ranges, the Central Valley, and the Sierra Nevadas where they lay their eggs on the resurgent milkweed flora and produce a spring generation. The extent to which they, or later generations, migrate over the Sierra Nevadas and eastwards to the Rocky Mountains is poorly understood. Monarchs that overwintered in Mexico remigrate at the end of March and early April to the Gulf Coast states where they produce a new spring generation on the southern milkweeds. A few of the overwintered monarchs probably migrate as far north as Canada. The large new generation produced in the south in April and early May flies northwards to southern Canada, laying eggs along the migration routes. After the first spring and two or three subsequent summer generations, the monarchs enter reproductive diapause and begin migrating southward to their respective overwintering sites. Spring remigrations of the eastern population over the Gulf of Mexico and through Cuba remain open to question (revised, originally from Brower & Malcolm 1991).

from the points of release and concluded that there is a bi-directional spring migration away from the southern California coastal overwintering sites: one northwesterly, the other easterly. Wenner (1994) reanalyzed these data and convincingly argued that the purported bidirectional distribution can not be statistically differentiated from random headings (letter from A. Wenner to W. Sakai, copy to LPB, 15–23 November 1994; LPB letter to Wenner, 15 January 1995). Nevertheless, the data established that 37 monarchs flew distances of 100 to 465 km from their overwintering sites, including flights northward through the Coast Ranges, over the Coast Ranges both to the Sierras and northward through the Central Valley, and eastwards into the San Gabriel and San Bernadino Mountains. Until it is technically possible to follow the tracks of large numbers of individual monarchs, we may be unable to distinguish a directional spring remigration from a random spring dispersal in California (the same criticism, in fact, applies to the spring remigration from Mexico).

Based on the information now available, the fall and spring migration patterns of the western population of the monarch are assumed to be as shown in Figs. 1A and 1B. Future tagging studies of the western population should concentrate on better understanding the fall migration throughout the western states to the numerous California overwintering sites.

Early Speculations on the Overwintering Areas of the Eastern Migration

Williams' (1930) collation of the literature through 1924 established that a fall migration of the monarch occurs east of the Rocky Mountains from Alberta to Maine, and southward to the Gulf Coast states from Texas to Florida, an area of about 8.3 million square km. Continuing to piece together the accumulating reports, Williams' subsequent summary maps (1938, Fig. 1, p. 218; Williams et al. 1942, Fig. 20, p. 172) supported the initial hypothesis that there are two migratory populations of the monarch in North America, one east and the other west of the Rocky Mountains, with overwintering areas in Florida and California, respectively. In the *Lepidopterists' News* of the newly founded Lepidopterists' Society, Williams (1949:18) called for more information on the overwintering sites: "In the south the butterflies hibernate in masses on trees. Such locations are known in southern California and in Florida, usually very close to the sea. What other areas are there? Are there hibernating areas along the Gulf Coast in Alabama, Mississippi, Louisiana or Texas? Are there any inland localities? What happens to the butterflies that fly south through Texas in the fall? Do they go into Mexico? If so, do they hibernate there, or remain active, or breed?"

The ensuing failure to confirm any overwintering sites along the Gulf Coast west of Florida led Williams (1958:13) to raise the possibility of three separate North American migrant populations: a western one overwintering in California, a second one overwintering along the Florida Gulf Coast (perhaps including Louisiana), and, as originally suggested by Brooks (1907, 1911), a third one migrating through Texas to overwinter in Mexico (see also Zahl 1963).

Early in his career, Urquhart (1949) proposed an even more complex hypothesis involving four overwintering areas for the eastern monarchs: (1) some overwinter in aggregations in Florida; (2) others overwinter as scattered individuals across the Gulf Coast States; (3) others must migrate to overwinter in Mexico and beyond; (4) while still others migrate westwards across the southern states to join the overwintering clusters in California.

The idea that eastern monarchs might migrate to California was potentially important because it departed from Williams' hypothesis of separate eastern and western populations and effectively considered *all* North American monarchs to be part of a single population. Urquhart kept the idea alive for the next 24 years (1965a, 1965b, 1966a, 1973a, 1973b), but recaptures of tagged butterflies did not provide evidence one way or the other. The idea thus stagnated until given a novel twist by Malcolm and Zalucki (1993b) in the general conclusions to their book (1993a:398): "Monarchs in California could be a sink population, continuously maintained by eastern monarchs as a source population." This seems unlikely because monarchs breed extensively at the lower elevations in the Coastal Range, the Sierra Nevada, the Cascade Range and in the Central Valley in California (Brower et al. 1982, 1984a, 1984b).

Given the fact that it is still unresolved whether any monarchs from the eastern population fly to the overwintering colonies in California, it seems prudent to cease making experimental transfers of monarchs between the eastern and western populations (Urquhart & Urquhart 1964, Cherubini in Anon. 1992). The fact that several of the transfers survived and were recaptured suggests that the releases probably already have resulted in interbreeding. This could confuse interpretations of classical morphological analyses as well as the new molecular and biochemical techniques that could be used to resolve this important biogeographical problem. My colleagues and I have recently written on the potential dangers of making such transfers (Brower et al. 1995).

Does Overwintering Occur in Peninsular Florida and Along the Gulf Coast?

Thaxter's (1880) report of overwintering butterflies along the Gulf Coast of Florida together with Bush's discovery of well defined overwintering colonies in California (in Riley & Bush 1881, 1882) biased subsequent workers into thinking that the eastern monarchs overwinter in the Gulf Coast states (Williams 1930, 1938, 1949, 1958, Urquhart 1960). Attempts over the years to obtain further evidence proved confusing and, at best, weakly confirmed the hypothesis. Thus Bromley (1928) reported great numbers of monarchs during January 1924 flying about, nectaring, and mating in the northern Everglades near Lake Okeechobee, and speculated that they represented an active overwintering population rather than resident breeders. While a lighthouse keeper reported "large numbers" of monarchs clustering on pines every winter from 1931–1937 on St. George Island (south of Apalachicola), other records between 1924–1937 only vaguely supported the idea that monarchs overwinter in Florida (Williams 1938:216–218). Fernald's (1939) discussion of the fall migrations southward through the Florida peninsula (rather than westwards along the Gulf Coast) stated that monarchs generally arrive in the Orlando area early in November. They then disperse, effectively disappearing by February, and reappear at the end of March or early April. The Hodges' data in Beall (1952) on migrations along the Atlantic Coast through Indialantic (about half way down the Florida peninsula) corroborated this timing. Fernald (1937) earlier had reported monarchs breeding in the Orlando area during January, and was clearly struggling in his 1939 paper to understand exactly when and where these migrants overwinter. He suggested that they may continue to Key West and even possibly to Cuba. What little is known of the phenology of monarchs in the Florida Keys weakly supports this hypothesis (Leston et al. 1982).

In an attempt to clarify the Florida situation, in January 1956 Urquhart (1960:302–307) searched for clusters from the Atlantic to the Gulf Coast near Tampa, without success. Correspondents' information, gathered during the 1950s, but frequently presented without definite dates by Urquhart, provided conflicting evidence. Thus Kimball reported few monarchs in Sarasota; Smith recounted large but abruptly disappearing clusters on oaks south of Tampa; Stiles traveled from the island of Captiva, south of Tampa, to Houston, Texas looking for clusters but found none. In contrast, Harris noted large numbers of monarchs forming loose aggregations on pines on Captiva on 5 November; and Stoddard reported several aggregations in a ten acre tract of young pines on Bald and Alligator Points on 4 November 1954 (these two Gulf Coast points are 56 km southwest of Tallahassee, about one mile west of Lighthouse Point in Franklin County). During the first week of February 1956, Harris and Stoddard returned to Alligator Point (Urquhart 1957:25–26) and tagged 1,000 of 1,500 clustering butterflies that they found clinging to the branches of the pine trees in four separate groups. Baker (1978:428) apparently interpreted these fragmentary observations to indicate extensive overwintering along the Gulf Coast and in Florida. It seems likely that he also was influenced by Williams' maps (1938:218, and Williams et al. 1942:172) showing five Gulf Coast overwintering sites.

Between 27 November 1981 and 20 February 1982, Brower and Calvert (Brower 1985a) monitored wintering clusters of an estimated 2,000 monarchs in a dense grove of pines on the northern part of Honeymoon Island, off the Gulf Coast west of Tampa. Other reports (including Urquhart 1966a) provided no further evidence of extensive overwintering aggregations in Florida, and a recent study suggests that the Brower-Calvert observations may have been made during an exceptional season (Cherubini 1994).

As far as I can glean from the literature, no winter aggregations have been reported along the Gulf Coast in Alabama, Mississippi, Louisiana or Texas (Bromley 1928, Williams 1938:218, 1949, Lambremont 1954, Teale 1954, Mather 1955, Mather & Mather 1958, Urquhart 1957, 1958, 1960, 1966a, Kimball 1965). Urquhart (1960), and numerous authors who subsequently cited him, clearly confused temporary bivouac clusters made by the fall migrants with true overwintering clusters. Other examples of this confusion included clusters seen at Lake Pontchartrain in Louisiana in October 1938 and November 1941 (Beall 1946), and clusters reported along the coast of western Mississippi at the end of October 1923 (Lyle, in Williams et al. 1942:169).

CAN OVERWINTERING OCCUR IN PENINSULAR FLORIDA AND ALONG THE GULF COAST?

Many monarch adults are killed by freezing during winter storms at the Mexican overwintering sites (Calvert & Brower 1981, Calvert & Cohen 1983, Calvert et al. 1982a, 1982b, 1983, 1984, 1986, Alonso et al. 1992). Following up on these studies, Anderson (in Brower 1987, 1990), and Anderson and Brower (1993) experimentally determined the temperature at which adult monarchs freeze to death. When there was no surface water on their bodies, 50% of the butterflies were killed at approximately −8°C, and 100% were killed at −14°C. If, on the other hand, their wings and bodies were wet, they lost at least half of this freezing resistance i.e., 50% died at −4°C and 100% died at −8°C. If the forest canopy above the butterflies has been thinned by wood harvesting, further heat is lost due to thermal radiation from the monarchs' bodies to the cold night sky, and even more freeze (Alonso et al. 1992). This is because the monarchs' body temperatures under open clear sky actually fall below the ambient temperature (Anderson & Brower, in press). A recent study by Larsen and Lee (1994) discovered that wet monarchs freeze faster than dry ones, adding to the importance of the sheltering effect of the intact Oyamel fir forest. The lowest temperature we have recorded in Mexico was in a treeless area near a Sierra Chincua colony on a clear night, when the temperature on the ground reached −8°C (Alonso et al. 1992).

What is the frequency and intensity of freezing during the winters along the Gulf Coast states, including Florida? The extreme one-time minimum temperatures recorded for at least 73 years through 1964 (except for Mobile, circa 25 years through 1963) were: Tallahassee, Florida, −16.7°C; Mobile, Alabama, −11.7°C; New Orleans, Louisiana,

−13.9°C; Houston, Texas, −15.0°C; and Brownsville, Texas, −11.1°C (Conway et. al. 1963, Bair 1992). A more detailed analysis of Jacksonville data for 150 years through 1985 indicated 24 winter freezes exceeding −6°C, 12 exceeding −8°C, and two exceeding −12°C (Chen and Gerber 1985). The all-time historical low was −15°C in January 1985. Indeed, Florida winters are characterized by frequent intrusions of Arctic air masses that are forced into the peninsula by southerly loops in the jet stream. Equally important is the fact that the leading edges of these cold fronts are generally preceded by rain (Johnson 1963, Chen & Gerber 1990).

Combining freezing records from Jacksonville with the monarch freezing point data leads me to conclude that about once each decade weather conditions in northern Florida would result in 50% mortality if the butterflies remained dry, or 100% mortality if they were previously wetted by rain. Severe freezes also occur farther south in the Florida peninsula. Thus, in Tampa the 75 year low through 1964 was −7.8°C. Such a winter freeze apparently killed monarchs at Davenport in central Florida during the 1937–1938 season (Colvin, in Williams et al. 1942:167). These data indicate that overwintering along the Gulf Coast from Northern Florida to Texas would be precarious, and in the long term, stable overwintering in this region probably can not be favored by natural selection.

The probability and severity of freezing is less in the areas south of Tampa, including the Everglades (Chen & Gerber 1985, 1990, Fig. 2.4). It therefore might be assumed that overwintering is possible in south Florida. However, here monarchs are confronted with a different problem: most of the time the weather is warm, with the consequence that the butterflies must become reproductively active (evidence in Brower 1985a, Table 1). When this occurs, the hormonal balance is shifted and the ability to migrate northwards almost certainly would be lost (see below). Thus, any monarchs that terminate their migration this far south will probably be incorporated into the local breeding populations. This appears to be occurring in a monarch population immediately northwest of the Miami airport, as described in Brower (1985a) and Malcolm and Brower (1986). Overwintering per se in southern Florida thus seems impossible.

I conclude that the sporadic observations made of monarch clusters over the past 150 years from Florida to Texas, together with the periodic freezes that must decimate them, provide very strong evidence that the southern Atlantic and Gulf Coastal states, including northern Florida, cannot and do not serve as safe, long term overwintering areas for the monarch.

FURTHER CONFUSION: WINTER BREEDING IN FLORIDA, ARIZONA, CALIFORNIA—AND THEREFORE MEXICO AS WELL?

Although Williams (1949) began questioning whether monarchs that migrate through Texas to overwinter in Mexico might possibly breed there, he subsequently (1958:108, 176) returned to his earlier position that they do not. Urquhart's data (1960:174 vs. 299–305) remained ambiguous. Soon thereafter, Brower (1961, 1962) reported monarch larvae in south central Florida during January as well as extensive breeding in the same area during the last week of March through mid April. Funk (1968) then reported winter breeding in southwestern Arizona, and Urquhart, Urquhart and Munger (1970) stated that they had found another continuously breeding population in southern California. These observations clearly challenged Williams' (1958) contention that monarchs do not breed in their purported overwintering range.

During January and February 1969, the Urquharts traveled in search of monarchs from Texas southward to the Chapala Lake area near Guadalajara in Jalisco, Mexico (Urquhart & Urquhart 1976e). This area is considerably west and north of where the overwintering sites would eventually be discovered. They reported that "during the months of January and February there were no monarch butterflies throughout southwestern Texas and Mexico north of Mexico City" (p. 439). Although suggesting that the butterflies might "remain in some obscure area of Mexico," it is clear from their new map and its caption that the discoveries of populations breeding during the winter in Florida, Arizona, and in southern California had begun to shift their thinking. Instead of envisioning passive overwintering colonies similar to those in Pacific Grove or Apalachicola, they now speculated that the fall migrants of the eastern population might end up breeding as far south as the Gulf of Tehuantepec in Mexico or even in Central America, while the western population might end up breeding as far south as Baja California.

Based on the recapture of one tagged monarch in San Luis Potosi (about 275 km north of the overwintering sites), and another near Mexico City, the Urquharts (Urquhart 1973a, 1973b) appear to have settled on the hypothesis that the terminus of the fall migration of the eastern population of monarchs must be southern Mexico or Central America. Speculating on the spring remigration, Urquhart said "we are of the opinion that the same individuals do not return, but their progeny do" (Urquhart 1973b:14). He then proposed that a new generation of monarchs born in Mexico and Central America flies north to Texas, there to produce a second, new generation in the spring, which in turn recolonizes the northern range. The Urquharts appear to have maintained this position even after the overwintering sites had been discovered. Thus, a 30 September 1975 newspaper article describing their research stated: "Few if any of the monarch butterflies which migrate south in the fall ever return. Most of those which come north in the spring are the children, or even the grandchildren of those who left the previous autumn" (del Vecchio 1975:20). Ordish (1977), a popularizer of science, wrote a semi-fictional account of monarch migration in eastern North America (see Brower 1977b), and stated that the butterflies overwinter south of the tropic of Cancer in the eastern Sierra Madre Oriental mountains. His statement appears to have been based on Rzedowski's (1957) earlier report of monarchs migrating along these mountains (see above).

The Urquharts' calls for help in locating the monarchs were published in Mexico City during February 1973 in English (Urquhart 1973a, 1973b) and Spanish (according to Urquhart 1987:155; see also de Montes 1975). Most significantly, Urquhart concluded each article with a request to naturalists in southern Mexico and Central America to join their tagging team "in order to obtain data to solve . . . (this) most interesting yet perplexing problem." The Urquharts' emphasis was on solving the spring remigration and clearly no one, including me (e.g., Brower and Huberth 1977), had any inkling of the incredible nature of the overwintering sites before November 1973.

DISCOVERY OF THE SIERRA PELON AND SIERRA CHINCUA OVERWINTERING SITES IN MEXICO

Although the well known Mexican poet, Homero Aridjis (1971), mentioned monarchs flying out of what we now know is an overwintering site on Cerro Altamirano in northern Michoacan (described in Calvert & Brower 1986), scientific resolution of the major eastern overwintering sites was achieved by two research associates of the Urquharts, Kenneth and Cathy Brugger. Because it is not clear from any of the Urquharts' publications (through Urquhart 1987) or from press releases (e.g., Del Vecchio 1975, Rensberger 1976) exactly when or where the Bruggers discovered the butterflies, I here attempt to reconstruct the sequence of events.

Kenneth Brugger, an American citizen working in Mexico, read one of the Urquharts' research notices and, according to Urquhart (1976b), volunteered to help in a letter to Urquhart dated 26 February 1973. On 6 November 1973, while Brugger was driving through the mountains west of Mexico City, he saw monarchs being pelted out of the sky by hail (Herberman 1990). In their annual newsletter summarizing the 1973 observations, Urquhart and Urquhart (1974:2) tantalized their readers with the statement that Ken Brugger of Mexico City was investigating the presence of monarch butterflies west of Mexico City and that "we are assured that somewhere in this general area the monarchs from the eastern United States and Canada spend the winter months." This finding also was referred to by de Montes (1975).

With the Urquharts' support and encouragement, Brugger and his Mexican wife, Cathy Aguado, finally discovered the first overwintering colony in January 1975. The Urquharts briefly reported the discovery in their 1975 annual newsletter, which in turn was quoted in a New Jersey newspaper by del Vecchio on 30 September 1975. Given the *New York Times'* frequent editorials and articles on the monarch (Anon. 1973, 1975, 1976, Sullivan 1973, Panzer 1975), I find it enigmatic that this newspaper, in particular, did not pick up on the discovery. The real impact of the Mexico findings came only after release of the August 1976 issue of the *National Geographic* magazine (Urquhart 1976b), followed by two scientific publications (Urquhart & Urquhart 1976c, 1976d).

Although Urquhart and Urquhart (1977a) gave 9 January 1975 as the discovery date, Herberman (1990:30) interviewed the Bruggers and determined that they had located the colony on 2 January 1975 (phone conversation, E. Herberman to LPB). According to Herberman, the initial colony was on Cerro Pelon, a 3,500 m high mountain in the Transverse Neovolcanic Belt, about 120 km west of Mexico City (see Calvert & Brower 1986 for the exact location of this site that we called *Sierra Pelon*).

Urquhart (1976b:173) wrote that "on their 1975 discovery trip, the Bruggers found two nearly equal concentrations a few miles apart." By piecing together information from Calvert's and my research and from the Urquharts' publications, I have deduced that this second site was the *Sierra Chincua* colony. Urquhart and Urquhart (1976c:157) stated that two butterflies were recaptured "at the overwintering sites" in January 1975. One of these recaptures, of a monarch tagged by Mrs. C. Emery in Nevada, Missouri on 9 September 1974, was made at "Monera Alta, Michoacan, Mexico" (Urquhart & Urquhart 1975:10; 1976c:157). Calvert and Brower (1986) determined that the *Mojonera Alta* is a large stone boundary marker near the summit of the Sierra Chincua, a separate mountain range about 30 km NNW of Sierra Pelon. In both the 1976–1977 and the 1977–1978 overwintering seasons, we found a large monarch colony about 2 km west of the Sierra Chincua marker, on the north facing slope of the Arroyo Zapatero (Calvert & Brower 1986). The Mojonera Alta is located at the intersection of the N–S coordinate 76 and E–W coordinate 64 as shown in Anonymous (1987). Thus the Emery butterfly had to have been recaptured by Brugger, in January 1975, near the Mojonera Alta, in the Sierra Chincua.

Further light can be shed on the history of the discovery by weaving together information in the Urquharts' 1975 annual newsletter, in the August 1976 *National Geographic,* and in a richly illustrated article by photographer Albert Moldvay, published nearly 6 years later in *Westways* magazine (Moldvay 1982). The Urquharts (1975:3) stated, after the Bruggers' discovery in January 1975, that "The National Geographic Society sent one of their official photographers to the site." According to Moldvay (1982:22), Bob Gilka (then Director of Photography of the magazine) telephoned him in Mexico in January and said "The wintering grounds of the Monarchs have been discovered." Moldvay's assignment was "to picture this sensational discovery of a mountaintop covered with migrating monarchs." Joining up with Ken and Cathy Brugger, and a guide named "Juan Sanchez," the four ascended the mountain. At the top, Moldvay "discovered a grove so thick with butterflies that I shouted for Cathy to come and pose among them. Soon she was as thickly covered in orange as the surrounding tree trunks."

Comparing the two articles, it is clear that two photographs in *National Geographic* and one in *Westways* are similar shots of Cathy posing amongst the monarchs on the Sierra Pelon (verified in Herberman 1990:30–31). That the mountain was the Sierra Pelon, and not the Sierra Chincua, is certain because another of the photographs in the *Westways* article (p. 22) is the valley below Pelon's western slope which I have ascended on two separate expeditions. To avoid future confusion, it should be noted that the guide "Juan Sanchez" in *National Geographic,* photographed by Bianca Lavies, is a different person than the guide "Juan Sanchez" shown in Moldvay's article. While Moldvay's "Juan Sanchez" presumably lives at the foot of Sierra Pelon, the man depicted in *National Geographic* is actually Raphael Sanchez who lives in Angangueo, the town below the Sierra Chincua colony. The Angangueo "Juan Sanchez" subsequently worked with Monarca AC of Mexico City, as well as with our research group. Because of his long commitment to the monarchs, Raphael Sanchez was awarded a citation by His Royal Highness Prince Philip, Honorary President of the World Wildlife Fund, in a ceremony that I attended in February 1988 in the Sierra Chincua.

From the above, it is now clear that the Moldvay photographs in the original 1976 *National Geographic* article were taken in the Sierra Pelon Colony during January 1975 with the Bruggers, while the Lavies photographs were taken at the Sierra Chincua Colony in January 1976 during the Urquharts' first expedition to the overwintering sites. Obfuscation of the facts surrounding the discovery of the overwintering sites, as we shall now see, was an unfortunate consequence of a policy decision made by the National Geographic Society.

THE URQUHART-BROWER SAGA

During the early 1970s I began a collaboration with James Seiber and Carolyn Nelson at the University of California in Davis to develop our previously described cardiac glycoside fingerprinting technique. In January 1973 I sent Urquhart a reprint of our study (Brower et al. 1972) comparing the cardiac glycoside content of various monarch populations in the east. In my letter I asked: ". . . do you know of any clustering sites in Mexico?" (LPB letter to Urquhart, 22 January 1973). He replied, "If we do find the areas of concentration we will certainly be able to arrange for specimens to be sent to you, or, if you wish, give you exact locations and names of the persons to contact" (FAU letter to LPB, 9 May 1973).

Because the thought of monarchs overwintering in Mexico had begun to tantalize me, I had also written to Dr. Eduardo Welling in Mexico about the migration, saying, "It really seems as if the migration is to a large extent a North American phenomenon in the Monarch butterfly. It seems likely that there must be some vast overwintering areas in Northern Mexico and that they do not just keep going southward" (LPB letter to Eduardo Welling, 9 September 1973). During the fall of 1973 and the spring of 1974 while on sabbatical at U. C. Davis, I began observing monarchs in their overwintering groves in California, and I decided to produce a film that would tie together the migration biology with our chemical studies (Brower & Huberth 1977).

In late 1974 Urquhart kindly sent me *Asclepias* seeds from Mexico (apparently that Brugger had collected, see Urquhart & Urquhart 1974). Without knowledge of the Bruggers' 2 January 1975 discovery, I wrote to thank Urquhart for the seeds and asked: "Have you found where the Monarch butterfly overwinters in Mexico yet? It must be a spectacular sight to see" (LPB letter to FAU, 8 January 1975). Because he did not answer this letter, and because his Annual Newsletter (Urquhart & Urquhart 1975) had announced the discovery, I again called him on 8 September 1975 and asked him to share the location of the site with me. He indicated that he could not divulge its location prior to publishing the *National Geographic* article, but that he would be able to do so after the discovery was in print (LPB record of phone conversation, and LPB letter to FAU, 11 October 1976).

Increasingly frustrated, I phoned the National Geographic Society in December 1975 and spoke to Mary Smith about whether they would share the location of the site. In a gracious letter (M. Smith letter to LPB, 10 December 1975), she indicated that the Society had adopted a policy not to divulge the location of the colonies prior to the publication of the discovery in their journal. I replied to her letter (LPB to M. Smith, 18 December 1975) that "I would trust that the National Geographic Society would, after having obtained . . . priority upon the article, disclose to bona fide scientists the information to pursue studies which might in fact make it easier to result in the ultimate protection . . . of the . . . monarch."

Following the Urquharts' (1976c) publication in the 22 September 1976 issue of the *Journal of the Lepidopterists' Society*, I wrote Urquhart (LPB letter to FAU, 11 October 1976) congratulating him on discovering the overwintering monarchs in Mexico, reminding him of our 8 September 1975 conversation, and again asking him to share the location of the colonies. I also invited him to Amherst College to present a lecture to us on his discovery. Since he did not immediately reply, and because neither the *National Geographic* nor the *Journal of the Lepidopterists' Society* articles gave details on the locations of the colonies, I began discussing the possibility of independently locating the sites with William H. Calvert, then a postdoctoral associate at the University of Massachusetts.

During the fall of 1976, Calvert and I attempted to deduce the general location of the sites from two crucial bits of information in the two Urquhart articles: (1) "At 10,000 feet, as we walked along the mountain crest, our hearts pounded" (Urquhart 1976b:166); and (2) "The overwintering colony . . . was located . . . in the northern part of the State of Michoacan, Mexico" (Urquhart and Urquhart (1976c:153).

In early December, Urquhart replied to my October letter (FAU letter to LPB, 3 December 1976) indicating that he had met with the National Geographic Society in August 1976 and that members of the editorial staff, President Payne, and others had "agreed that the site should not be divulged since it was anticipated that many people, collectors, film makers, etc. would wish to visit and, as happened in other similar situations, destroy it . . . I would suggest to you, since the Mexican site is not available, that you examine the . . . monarchs that pass along the . . . Gulf Coast . . . during October and November. These monarchs will eventually reach Mexico and you would accomplish the same results as visiting the area" (see also Urquhart & Urquhart 1977c, Urquhart 1978).

I replied (LPB letter to FAU, 14 December 1976) that I was "greatly distressed" by his letter. I explained that I was keen to visit the overwintering site to complete my 30-minute documentary film (Brower & Huberth 1977) which I had begun in California, and that I wanted the animated migration map to depict the migration to Mexico accurately. In addition, samples from the newly discovered overwintering sites would be of great interest for the fingerprinting analyses that I was pursuing with my honors students at Amherst College. I ended my letter as follows: "Perhaps in view of this letter, you might review your position and consider sharing the location of the site with a fellow scientist, who, like you, is equally keen in conserving the site from modern depredations of human society. Again, I congratulate you upon your discovery."

Motivated even more strongly by Urquhart's 3 December letter, Calvert and I obtained a copy of a 1:1,000,000 topographic map (Anon. 1959) that included the Michoacan region of Mexico. We circled all the areas on the map above 10,000 feet in the general area suggested by the Urquharts' two articles. Then, armed with copies of the map, Calvert, accompanied by John Christian, Victoria Foe, and Michael Dennis, left Austin, Texas for Mexico on 26 December 1976. On New Years' Eve, Calvert telephoned me from Mexico at my home in Amherst, Massachusetts: with the help of a local guide who was a nephew of Municipal President Manuel Arriaga Nava from the town of Angangueo, they had located the Sierra Chincua colony on 30 December 1976. Earlier that day, Mayor Nava had given Calvert written authorization to visit the area (copy in Brower files). According to Urquhart and Urquhart (1977c:3), Brugger had located this same site two days before Calvert and his colleagues had found it.

Following Calvert's return to Amherst, he, my technician Lee Hedrick and I mounted a second expedition and arrived at the Sierra Chincua site about 1500 hr on 22 January 1977. I summarized our observations in the May/June issue of *Natural History* (Brower 1977a) and later in the *Journal of the Lepidopterists' Society* (Brower et al. 1977). As fate would have it, we encountered the Urquharts and Bruggers tagging monarchs inside the colony. The Urquharts were bewildered by our arrival and initially treated us rudely, and then with hostility. After returning to Toronto, the Urquharts mailed a letter to their research associates dated (according to Anne Neale, in a letter to Robert Dirig) 3 February 1977. This letter incorrectly accused us of impropriety at the overwintering site, and subsequently generated vitriolic correspondence from some of the Urquharts' associates (including a letter to then-President John Ward of Amherst College).

Bayard Webster, a science writer for the *New York Times*, was aware of the brouhaha, and attended the annual banquet of The Xerces Society in New York City on 30 April 1977, hosted by Joan DeWind. After my invited talk and slide show, Webster and I discussed the allegations and I informed him of my forthcoming article in *Natural History* (published in June 1977). I subsequently provided him with several of my publications, a copy of field notes made at the Sierra Chincua, and copies of most of the aforementioned correspondence. In reviewing my *Nat-*

ural History article in the *New York Times* on 29 May 1977, Webster downplayed the rancor, stating that my article had "brought attention to a smoldering rivalry between two internationally known scientists."

Unfortunately, the *New York Times* index for 1977 embellished this: "Profs are keen rivals in longtime search for species' habitat" (Anon. 1977d:199–200). The negative aspects were amplified by Richard Barthelemy (1978), who had independently discovered the Sierra Chincua site in March 1977 (Barthelemy 1977; Barthelemy later joined our expeditions to the Sierra Chincua and we became good friends before he died from cancer in 1988). In early June, the world press succeeded admirably in turning the "rivalry" into a major conflagration (see for example: Anon. 1977a–c, Michelmore 1977, Hough 1977, Saenger 1977). Among the more inflammatory journalistic statements were those by Peter Wood (1977:56) in Time-Life's *Nature Science Annual* e.g., "The dispute may be settled by the Mexican government, which is now considering setting aside the area as a sanctuary, safe from the biologists' squabbles and other ecological perils." This was published after I was interviewed by phone, and over my objections to the draft statement (Charlie Clark letter to LPB, 24 June 1977; LPB letter to C. Clark, 13 July 1977).

In September 1977, the Urquharts mailed a letter and an eight page mimeographed "special report" to their research associates (Urquhart & Urquhart 1977c). The document bitterly attacked the *Natural History* article and falsely accused us of having followed Brugger into the site, and of purposefully starting a fire under the butterflies "to dislodge monarchs from their roosting trees to provide material for dramatic photographic shots. . . ." Calvert, Hedrick and I wrote Urquhart on 28 September 1977 explaining in detail how we had found the Sierra Chincua overwintering site, and that we felt he had misinterpreted our research activities. The Urquharts never replied either to this or to any of several other attempts to reconcile the situation.

In spite of initial urging from President Ward of Amherst, I chose not to respond in print to the Urquharts' accusations. In retrospect, this was a mistake, because the unrefuted allegations polarized the monarch community—the very group of people who, had they adopted a unified front, could have been far more effective at promoting conservation of the overwintering sites.

MONARCHS OVERWINTER IN THE OYAMEL FIR FOREST ECOSYSTEM LOCATED IN THE TRANSVERSE NEOVOLCANIC BELT OF MEXICO

Following our January 1977 expedition to the Sierra Chincua, Calvert joined my Amherst College research group and subsequently led several expeditions to determine the extent of monarch overwintering in Mexico. Calvert teamed up with Javier de la Maza, a prominent member of the Mexican Lepidopterists' Society, and they and others searched widely in central, eastern, and southern Mexico (de la Maza et al. 1977, de la Maza & Calvert 1993). By 1986 they had located a total of approximately 30 overwintering colonies on 9 separate mountain massifs, all between 70 and 170 km west of Mexico City in the states of Mexico and Michoacan (Calvert & Brower 1986, de la Maza & Calvert 1993). Their work confirmed that the overwintering phenomenon is intimately associated with Oyamel fir forests, *Abies religiosa* (H.B.K.) Schl. & Cham. (Pinaceae) (reviews in Brower 1985, Calvert et al. 1989, Brower & Malcolm 1991, Snook 1993a, Núñez and García 1993, see also Urquhart & Urquhart 1978a, 1978b, 1980, and Anon. 1981).

All of the sites known to us occur in a small area of *The Transverse Neovolcanic Belt,* a 50 to 100 km wide belt of volcanic mountains and valleys that extends for 800 km across Mexico between latitudes 19°N and 20°N. This is a rugged, beautiful and topographically complex region averaging about 2,500 m in altitude It contains hundreds of volcanic cones projecting into rich elevated valleys, including 13 of the highest peaks in Mexico, three of which exceed 3,650 m (Moore 1945, Goldman & Moore 1946, Raisz 1964, Arbingast et al. 1975). According to Thayer (1916), Garfias and Chapin (1949) and Duellman (1965), the Transverse Neovolcanic Belt originated during two periods of volcanism that accounted for most of the uplift as well as the volcanic peaks. The first period of volcanism occurred during the Miocene and affected all of Mexico, while the second began in the Pliocene and is still occurring in the Transverse Neovolcanic Belt.

The Oyamel forest is a specialized high altitude ecosystem that occurs as 13 vegetational islands on the higher peaks in Mexico and constitutes less than one half of one percent of Mexico's land area. Nine of these montane islands occur in the Transverse Neovolcanic Belt, three in the Sierra Madre Oriental, and one in northern Baja California (Leopold 1950, 1959, Arbingast et al. 1975, Anon. 1981). Because the Oyamel forest's general physiognomy is like that of northern Canadian forests, it is called a boreal forest ecosystem. According to Rzedowski (1978) and Manzanilla (1974), as summarized in Snook (1993a:365): "Today's fir forests in Mexico are relicts of extensive boreal forests that advanced southward as the cold climates descended to tropical latitudes during the periods of glaciation. . . In the 10,000 yr since the glaciers retreated, these forests have been displaced by temperate and tropical floras adapted to the warmer climatic conditions of today. Now only 40,000 to 50,000 ha of fir forests remain in Mexico. . . , distributed as isolated islands at elevations between 2,400 and 3,600 m. . . , where the cold climate excludes most other genera and permits the firs to dominate. This reduced area and patchy distribution pattern make the fir forest perhaps the most vulnerable to deforestation pressures of any type of forest in Mexico." Below the fir belt, various species of oaks and pines are abundant, whereas above the firs several other species of pines dominate up to the snow line (Loock 1950:32). The fir forest coincides with a summer fog belt and is damp, with mosses and lichens on the forest floor, and a rich herbaceous and shrub understory growing in partly opened areas beneath the forest. On clear days throughout most of the winter, hummingbirds are commonly seen feeding on crimson flowers. For a wealth of new information on the vegetation associated with the monarch's overwintering areas in this fir forest ecosystem, see Snook (1993a) and Núñez and García (1993).

Survival of the monarchs from November through March depends on a balance of macro and microclimatic factors, such that the weather is: (1) cold enough to maintain the butterflies in a state of reproductive torpor, but not so cold as to kill them; (2) warm enough to maintain the integrity of their clusters, but not so warm as to result in excessive activity; and (3) wet enough to prevent desiccation and forest fires, but not so wet and cold as to preclude all activity (Brower 1985, Masters et al. 1988). The microclimate of these Oyamel forests shares many characteristics with the sea-level Monterey pine and *Eucalyptus* forests along the coast of California where the western population overwinters (Leong 1990, Weiss et al. 1991).

Contrary to expectation based on the aggregation behavior and sophisticated chemical defense of the monarch (Brower 1985), we discovered that two species of birds and one species of mouse are killing as many as one million butterflies in the overwintering colonies (Calvert et al. 1979, Fink & Brower 1981, Brower & Calvert 1985, Brower & Fink 1985; Brower et al. 1985, 1988, Glendinning & Brower 1990, Arrellano et al. 1993). We have hypothesized that these current high predation rates are due to the historical shift of larval feeding from the more toxic prairie milkweeds to *Asclepias syriaca*. As noted above, this milkweed increased in abundance following the plowing of the prairies and cutting of the eastern forests. *Asclepias syriaca* contains variable amounts of weakly emetic cardiac glycosides. Monarchs that feed upon it as larvae in the wild reflect this low toxicity and gradually lose the poisons as they age (Alonso-Mejia & Brower 1994). This presumably results in the ability of the birds and mice to feast on the butterflies.

As summarized by Calvert and Brower (1986, Fig. 1) and de la Maza and Calvert (1993), the principal overwintering sites are limited to perilously few mountain ranges in the center of the Transverse Neovolcanic Belt, overlapping the northern state borders of Michoacan and Mexico, between latitudes 19°20' and 19°45'N and longitudes 100°10' and 100°20'W. Within this tiny area of about 800 square km, five mountain ranges—the Sierra Chincua, Sierra Campanario, Sierra Chivati, Sierra Picacho and Sierra Pelon—have consistently harbored one or more overwintering colonies. Four smaller and less predictable overwintering areas also occur within a radius of 50 km of the main area: Contapec and San Andreas occur to the North, and Las Palomas and Herrada occur to the southeast, on the southwestern slope of Volcan Toluca (Xinantecatl = The Nude Man, Melgareio 1910; after major snowstorms and the passage of cold fronts, this 4,558 m high volcano is a magnificent spectacle.) De la Maza and Calvert (1993) discuss weak evidence for other colonies and migrations in southern Mexico and in northern Guatemala which may result from monarchs migrating across the Gulf of Mexico, or from Florida across Yucatan (see below).

NOMENCLATURE OF THE TRANSVERSE NEOVOLCANIC BELT

The nomenclature of the geographic location of the overwintering area in the volcanic highlands of central Mexico has been historically fluid (partly, I must confess, through my own writings). A serious error was made in the original *National Geographic* article which referred five times to the area as the "Sierra Madre" (Urquhart 1976b, see also Urquhart & Urquhart 1977a, 1977b). The eastern Sierra Madre Oriental and the western Sierra Madre Occidental (Figs. 1A and B), are two distinct mountain complexes which are much older than the volcanic highlands, having originated during the Laramide (Rocky Mountain) and Sierra Nevadan orogenies, respectively (see Arbingast et al. 1975 and Garver 1981 for maps that clearly depict the major mountain ranges of Mexico.) Although the Urquharts subsequently corrected their error, referring to the area as the "Neo-Volcanic Plateau of Mexico" (1978b: 1760, 1978c:134), the Hollywood-like ring of "The Sierra Madre" has proven difficult to expunge from the popular literature (e.g., Wood 1977, Pyle 1981, Ellis 1984, Shull 1987, Peach 1988, Anon. 1991, Dalrymple & Gottfried 1995).

In my original description of the Sierra Chincua overwintering site, I referred to its location as *The Trans-Mexico Volcanic Belt* (Brower 1977a), which we changed to the etymologically incorrect *Trans-Volcanic Belt of Mexico* in Brower et al. (1977); to *The Volcanic Highlands of Central Mexico, The Sierra Volcanica Transversal* and *The Transvolcanic Range of Mexico,* all in Brower (1985); and, finally, to the *The Transvolcanic Belt of Central Mexico* in Calvert and Brower (1986). Other authors' names for the region include *The Cordillera de Anahuac,* rejected in favor of *The Volcanic Province* (Thayer 1916), *The Transverse Volcanic Biotic Province* (Moore 1945, Goldman & Moore 1946), the *Sierra de los Volcanes* (Garfias & Chapin 1949), *The Great Cross Range* (Loock 1950), *The Neovolcanic Plateau* (Raisz 1964), *The Cordillera Volcánica* (Duellman 1965), *The Cordillera Neo-*

volcánica (Arbingast et al. 1975), *The Provincia Eje Neovolcánico* (Anon. 1981), *The Eje Neovolcánico Transversal* (de la Maza & Calvert 1993), and *The Transverse Neovolcanic Belt* (Núñez & García 1993). In honor of Dr. Leonilla Vasquez García who was one of the first Mexican scientists to visit the Sierra Chincua overwintering area, I propose that Lepidopterists settle on *The Transverse Neovolcanic Belt*.

HISTORICAL AND CURRENT ABUSE OF THE OYAMEL FORESTS

As Leopold (1950:511) pointed out, the land below these Oyamel forests has been abused by humanity since prehistoric times: ". . . the greatest part of the Mexican population has lived in the pine-oak zone with its healthy, temperate climate suitable for the cultivation of corn. As a result . . . natural resources of the southern uplands have been severely taxed and in some localities largely destroyed."

According to Loock (1950:29–32), the original *Abies religiosa* forests consisted of trees nearly 2 m in diameter and 50 m in height, far larger than trees we have observed in all the current overwintering sites. When these forests were less disturbed by humans, it is likely that monarchs overwintered in them more widely in the Transverse Neovolcanic Belt. In 1984, Monarca AC, a Mexico City non-governmental conservation organization largely supported by the World Wildlife Fund (Ogarrio 1993, Gottfried 1993, Monasterio 1993, Camus 1993) sponsored an extensive search of more than 60 oyamel forests across the entire Transverse Neovolcanic Belt. More than 60 potential overwintering sites were found "located in areas where intense commercial lumbering has resulted in the destruction of much of the original vegetation" (de la Maza & Calvert 1993:296).

A detailed documentation of the current pressures on the Oyamel forests, as well as suggestions for coping with them, are in Snook (1993a). Wood is being harvested in and adjacent to the current overwintering areas by local inhabitants for building their homes and sheds, for heating, and for cooking; commercial logging that is both legal and illegal is being conducted on a large scale, apparently at ever-increasing rates; and a cottage charcoal industry is developing.

The Decree issued by President Miguel de la Madrid in October 1986 (de Castro 1993) that supposedly protected five of the nine known Mexico overwintering sites has been violated at most sites. The Sierra Chivati was clear cut in 1986, the very year the decree was declared. Wood cutting is now focusing on the so-called buffer areas around virtually all of the colony core areas (Brower 1987, Calvert et al. 1989, Stevens 1990, Homero Aridjis in Nusser 1992, de Castro 1993, de Castilla 1993, Snook 1993a, Brower, Calvert & Alonso M., current observations through January 1995).

It is possible that these extensive forest disturbances are disorienting current generations of fall migrants. This may explain the temporary clustering sites and enigmatic migratory movements reported by de la Maza et al. (1977). I also have an uneasy impression, based on my observations of the spring remigration into north central Florida since 1981, that monarchs left the overwintering sites in Mexico abnormally early in the springs of 1994 and 1995.

Overwintering of the monarch butterfly in Mexico is clearly threatened (see below). Current statements in the popular press that the overwintering monarch numbers are "normal" in Mexico (e.g., Marriott 1995) are not cognizant that the outlying sites, to which tourists do not have access, may be collapsing. Bereft monarchs may well be aggregating at the few protected sites, giving a false impression of the total numbers that are actually overwintering.

SPRING RECOLONIZATION OF THE EASTERN BREEDING RANGE

The *modus operandi* of the spring remigration of the eastern population was debated vigorously in the 19th century. Observations made by Edwards (1878) in West Virginia led him to suggest that the overwintered individuals produce a succession of generations that move north over the spring and summer, while Scudder (1881) speculated that individual winter survivors move northward and recolonize the entire breeding range. Urquhart's (1960, 1965a, 1966a) summaries of his tagging program did not relsove the issue (Roer 1967:197), and by early 1973 Urquhart (1973b) proposed that the fall migrants themselves probably do not return from the south, but that their progeny do.

The discovery of the overwintering sites in Mexico effectively jettisoned the hypothesis that a fresh generation of monarchs reinvades the United States each spring and stimulated my research group to investigate the spring remigration (Brower 1985, Malcolm et al. 1993, Brower 1993). We formalized the two 19th century alternatives as: (1) Scudder's modified "single sweep hypothesis," in which winter survivors from Mexico fly to the southern United States, oviposit on the newly emergent *Asclepias* flora, and continue to fly northward to southern Canada ovipositing along the way; and 2) Edwards' modified "successive brood hypothesis," in which the winter survivors fly to the Gulf Coast where they oviposit extensively on the milkweeds, and then die. A new spring generation produced in the south then continues the migration northward to southern Canada, laying eggs along the way.

The departure of monarchs from the overwintering sites in Mexico occurs towards the end of March and early in April (Brower 1985, Calvert & Brower 1986). This timing is consistent with an earlier report of the spring remigration in eastern Mexico. On 22 March 1962 while driving along the eastern slope of the Sierra Madre Oriental in Mexico, Heitzman (1962) encountered large numbers of monarchs flying northward through the town of Ciudad Mante, in the State of Tamaulipas. The butterflies were drinking nectar from roadside flowers, and roosting was observed as early as 14:30 hr.

Malcolm, Cockrell and Brower (1993) determined that Edwards' successive brood hypotheses prevails, by comparing the cardiac glycoside fingerprints in four groups of monarchs: (1) fall migrants of the last summer generation, most of which we predicted had fed on *Asclepias syriaca*; (2) monarchs collected at their overwintering sites in Mexico; (3) monarchs that had flown back from Mexico in April to the Gulf Coast states of Texas, Louisiana, Mississippi, Alabama and Florida; and, crucially, (4) monarchs collected in early June across the northern tier of states, from Massachusetts through Wisconsin to North Dakota. We found that over 80% of several hundred fall migrant, overwintering, and returning coastal monarchs had the *A. syriaca* foodplant pattern. In contrast, only 6% of 629 butterflies collected along the northern tier in June had the *A. syriaca* pattern; 90% of them had fingerprints derived from southern milkweeds, including *A. viridis* and *A. humistrata*. These data clearly indicate that the majority of migrants returning from Mexico lay their eggs on the southern milkweed species and then die. Their children, imbued with the distinctive *A.viridis* or *A. humistrata* fingerprints, then continue the migration to the northern states. Thus Edwards' perspicacity of 1881 proved to be largely correct: monarchs recolonize eastern North America each spring by successive brood remigration (Fig. 1B).

I say *largely*, because fragments of data in the older literature have swayed me to believe that Scudder's single sweep remigration hypothesis should not be completely discarded. Shannon (1915) reported seeing old, faded monarchs on Long Island, New York in June and later (1954) reported several worn and faded monarchs of both sexes in Port Monmouth, New Jersey on 12 May 1916. If these butterflies were of the new spring generation produced in the Gulf states, they should have looked fresher, as were most of the monarchs collected in the Great Lakes region in early June as reported in Malcolm, Cockrell and Brower (1993).

Two of the earliest observations of spring swarming behavior (reported in Riley 1871:151) add credence to the single sweep hypothesis. The first was Stroop's observation of about 30 individuals on 31 March 1870 near Dallas, Texas (see also Stroop & Riley 1870). The second was made the very same spring in Manhattan, Kansas, where in mid-April

Wells saw large numbers of monarchs in a swarm coming "rapidly with a strong wind from the (sic) N.W. . . filled the atmosphere all around for more than an hour, sometimes as to eclipse the light." Riley accepted both reports on face value and made two critical assumptions: it was too early for milkweeds to have flushed out either in Texas or in Kansas, and the "bevies" in both areas were moving southwards. Tutt (1900: 209) questioned the direction of flight of the Kansas butterflies saying "surely at this time of the year the flight should have been going to the north-west, not coming 'from' the north-west." Moffat (1901b:50) later reasoned that both of these groups were actually migrating northward in the spring, interpreting the seemingly incorrect direction as a consequence of the swarms having been caught up in a wind too heavy to fly against. He based this deduction on having personally observed individual monarchs in a gale that were being blown along with the wind.

We now know that the milkweeds would have flushed out by this time in Texas and Louisiana (Lynch & Martin 1993, Malcolm et al. 1993, Riley 1993), and that by mid April very early shoots would probably also have been available in Kansas (Orley Taylor, pers. comm. 1995). I think it likely that there may have been a large migration of monarchs returning to Texas from Mexico in the spring of 1870, and that some of the butterflies were blown northward just as the milkweeds were sprouting in Kansas. If the offspring of these early migrants survived, then a single sweep also would be indicated.

Three other reports of early spring remigrations in the north that also supported the single sweep hypothesis were as follows: during 1889 in the Red River Valley of Minnesota, monarchs arrived as early as 2 May (Lugger 1990); a more or less constant low flow of monarchs passed north or northwestward along Virginia Beach, Virginia from 18–30 April 1906 (Jones, in Clark 1941); and a large flock of hundreds of presumed monarchs were seen flying northward over Oklahoma on 9 March 1928 (Cleveland, in Clark 1941).

I predict that future research will establish that the successive brood recolonization is the major strategy employed by the monarch, but that a few individuals do manage a single sweep recolonization to the north. Many of these latter monarchs may overshoot the expanding northward wave of sprouting milkweeds and freeze to death. On the other hand, if they survive until the milkweeds have sprouted, they could gain a substantial temporal advantage. Both strategies may contribute to establishing many breeding colonies throughout the expanding spring range of the monarch. Long-term quantitative studies that monitor the timing and magnitudes of the spring movements of monarchs through key areas are needed to gain a fuller understanding of the spring remigration (e.g., see Fales 1977, 1984).

How Many Generations Are There in the Breeding Range?

The number of broods of monarchs produced at various latitudes was vigorously debated in the 19th century. Edwards (1876a, 1876b, 1878, 1881, 1888), Morton (1888) and Marsh (1888) provided strong evidence for multiple broods from West Virginia to southern Canada while Scudder (Scudder & Gulick 1875, Scudder 1881, 1889:741–742) stubbornly argued for a single brood throughout the monarch's range (see Tutt 1900:183–184). Riley (1878a, 1878b) believed there were three or more broods in the south, but only one towards Canada (see also Riley 1880b, 1890). It is curious that Scudder did not deduce that several generations were possible from Harris' early 19th century data, which Scudder himself had spent an enormous effort to collate and publish (Scudder & Harris 1869). Harris, a sadly frustrated Harvard librarian who had quit his medical profession in order, he hoped, to pursue entomology (Evans 1985), produced the first data on monarch development rates (Harris 1863, given in detail in Scudder & Harris 1869). If four days for egg development and four days for adult maturation following eclosion are added to Harris' recorded minimum of 23 days for larval and chrysalid development, a total of 31 days is obtained. It should therefore have been obvious to Scudder that more than one summer generation was possible in New England.

Moffat (1900a, 1901b, 1902b), who lived in southern Ontario, provided concrete evidence for more than one brood in the north, but also suggested an important alternative: because there may be more than a single wave of migrants returning from the south, there may be an overlapping of generations. In their highly influential book, *How to Know the Butterflies* (1904), John Henry Comstock, the first professor of entomology at Cornell University, and his wife Anna Botsford Comstock accepted that there are multiple broods: "The mother butterfly follows the spring northward as it advances as far as she finds milkweeds sprouting [and] generation after generation pushes on . . . as far north as Hudson Bay" (p. 205). Seitz (1924) also endorsed multiple broods, stating that there were up to four each year.

The emerging idea of a relay race involving successive generations was embraced by Ricker (1906:48) and Julia Rogers (1911), editor of the Nature Club Column of *Country Life in America*. However, lack of definitive evidence apparently was responsible for J. A. Comstock's (1927:58–59, 127–130) vague description of the spring recolonization (J. A. Comstock, no relation to Cornell's John Henry Comstock, was Director of Science at the Los Angeles County Museum and author of

Butterflies of California; Kendall et al. 1977:83–84). Clark and Clark (1951) again implied that there is a relay race and stated that there are four to six summer generations in Virginia. Urquhart (1960:60–62) attempted to deduce the number of generations at various latitudes and longitudes as well as the degree to which they overlap. Based on new development rate data (Rawlins & Lederhouse 1981, Zalucki 1982), Cockrell, Malcolm, and Brower (1993) calculated that there is probably a maximum of five generations in the eastern population, which would include two generations in the southern U.S.A. and three northward to Canada over the late spring and summer. More quantitative data are needed to establish the number of broods and the degree to which they overlap throughout the range of the monarch in eastern and western North America.

FLUCTUATIONS IN THE NUMBERS OF FALL MIGRANTS

The accumulated anecdotal evidence on the eastern population over the past 125 years indicates variability in the numbers of monarchs migrating southward. Examples included a large migration in the fall of 1872 over Cleveland where no migrations were reported during the next three years (Ison, in Anon. 1875), and another large migration through Hamilton, Ontario in 1899 that had been preceded by three autumns when the monarchs in the same area were comparatively scarce (Moffat 1900a, 1900b, Bethune 1900:101). Other instances of year to year variability, or years of notably large numbers, were reported by Reed (1869), Scudder and Allen (1869), Saunders (in Riley et al. 1875), Lugger (1890), Brooks (1911), Thoms (1911), Stoner (1919), Webster (1892, 1912, 1914, 1915), Hutchings (1923, in Felt 1928:101), Williams (1930, 1938), Clark (1941), Williams et al. (1942), Brown (1950), Ferguson (1955), Urquhart (1960, 1974), Hoying (1972), Anon. (1973), Sullivan (1973), Brewer (1974), Jackson (1974), and Yeager (1974).

We therefore have a substantial but completely anecdotal literature that the numbers of butterflies in the fall migration of the eastern population fluctuate from enormity to rarity, without understanding why this is so. Reconstruction of at least a crude picture of the fluctuations back to the 1880s could probably be done by systematically organizing records from the literature (including the annual field season summaries in the *News of the Lepidopterists' Society*), gleaning information from local newspapers, scouring unpublished records of various state parks and wildlife sanctuaries, interviewing naturalists who keep accurate records, and computerizing the Urquharts' extensive files.

Urquhart (1960:69) had interpreted the available data as indicating a 6–7 year cycle which he initially attributed to weather, and later to a virus (1966b:1970, see also Sullivan 1973), which another author suggested may have been a bacterium (Anon 1971). Urquhart (1987: 95) recently concluded that "there is no true cycle, but rather the fluctuation in population is irregular, and periods of scarcity and abundance occur in any year." He vaguely attributed the fluctuations to a dynamic interaction of the monarch with summer temperatures, storms, and the waxing and waning of polyhedrosis virus resistance.

My field studies in the eastern breeding range over the past 38 years and at the overwintering sites in Mexico over the past 17 years lead me to conclude that monarchs are not often subjected to heavy disease and parasitism in wild populations. I hypothesize that this is because the almost continuous migratory movement of the adult butterflies from March through October allows them to escape the build-up of viral and bacterial pathogens and hymenopteran and dipteran parasitoids. There is, however, a severe protozoan pathogen in the California population that may currently be decimating the colonies (Brower et al. 1995).

I propose that years of small autumn migrations are principally a consequence of storm-caused mortality at the Mexican sites the previous winter followed by overcast, wet and cold weather during the spring and summer breeding in the U.S.A. and Canada. Since the 1976–1977 overwintering season in Mexico, we have witnessed two winter storm systems that caused severe mortality. During the 1980–1981 season, approximately 42% of the monarchs were killed in the Sierra Chincua colony during a period with snow, rain and freezing temperatures (Calvert et al. 1983, Calvert & Brower 1986). In February 1992, prolonged rainy weather during January and February was followed by a severe freeze that killed more than 80% of the butterflies at the Herreda overwintering site (Brower in Culotta 1992, Brower et al. unpublished data).

Variations in temperature, cloud cover and rainfall throughout the monarch's breeding range will affect both the milkweed and nectar sources. Climate, therefore, is probably the major determinant of both the success of breeding in each generation as well as the number of generations produced. If severe freezing at the Mexican overwintering sites were followed by wet and cold weather in the spring and summer breeding ranges, then I would predict fewer and smaller generations and a reduced fall migration. Dry, hot summers also would be detrimental. If, on the other hand, a mild winter in Mexico were followed by warm and clear weather across the eastern U.S.A. and southern Canada, with sufficient rainfall to optimize the growth of milkweeds and nectar resources, I would predict a large fall migration.

Correlating past and future annual variation in the abundance of fall migrants with historical weather data will undoubtedly prove informative. Standardized, quantitative estimates both of the colony sizes in Mexico and the numbers of butterflies migrating in the spring and fall are greatly needed to monitor the impact of humans on the monarch's breeding and overwintering habitats, as will be discussed below.

Over the next few years, I predict that the size of the monarch's fall migration will dwindle because of the increasing use of herbicides across North America (Lever 1990). These chemicals kill both the milkweed larval foodplants and other herbaceous plants that serve as nectar sources throughout the monarch's annual cycle. In 1993, an estimated 4.6 billion dollars were spent on 620 million pounds of herbicides in the U.S.A., and usage of these chemicals exceeded the combined use of all other pesticides, including insecticides, fungicides and other undesignated biocides (Aspelin 1994). The intended goal of herbicide use (now sprayed by over one million "certified applicators") is to kill all competing plants over tens of millions of hectares of croplands.

EVALUATION OF THE "ABERRANT EAST COAST MIGRATION" HYPOTHESIS

Prior to announcing the discovery of the Mexican overwintering sites (Urquhart 1976b, Urquhart & Urquhart 1976c), Urquhart and Urquhart (1976b) had proposed that the fall migration along the eastern coast of the United States is "aberrant." By this they meant that the migration was off of the direct southwesterly route to Mexico. While this hypothesis seems to have crystallized as a result of the Mexico discovery, they attributed it to tagging recoveries, personal observations, and collaborators' reports.

According to the initial hypothesis (Urquhart & Urquhart 1976b), there is only a meager migration through Florida, largely along the western side of the peninsula. Developing the idea further, Urquhart and Urquhart (1976d, Fig. 3) presented a map showing two fall migratory routes for the entire eastern population. The route flown by the majority of monarchs produced in the Great Lakes region is on a southwesterly course to the central Mexican overwintering sites (see also the extensive new directional data in Schmidt-Koenig 1985, 1993). The second route, which they now called "the migration route of the aberrant population" was hypothesized to be a subgroup of these butterflies flying southward over the Appalachians into Florida, thence to Cuba, the Yucatan, and Guatemala. In their next publication, the Urquharts re-drew their 1976b map (see Fig. 2, p. 1586 in Urquhart & Urquhart 1977a) to include a western Great Plains component of monarchs flying southeasterly to join with the main group migrating into central Mexico.

Two years later Urquhart and Urquhart (1979b, see also Urquhart, 1987:138–143) published a new set of recapture records and elaborately developed the hypothesis. Strong winds out of the west during the fall migration, they proposed, blow many monarchs off their main southwesterly course and drive them eastwards towards the Atlantic Coast (see also Gibo, 1986:178). Presumably, most of these monarchs recover their southwesterly flight orientation and eventually fly through Texas to Mexico. The rest of the butterflies, however, accumulate along the east coast and may then perform three possible so-called "aberrant migrations" across the open ocean. While the Urquharts' recapture data at best weakly supported their hypothesis, I believe that they were largely correct in postulating these three movements. However, I contend that what they called "aberrant migrations" should be called "eastern dispersal routes" for reasons that will become clear. The Urquharts' three dispersal routes are as follows.

Eastern Dispersal Route 1: Florida to the Yucatan and Central America. These butterflies are held to fly along the Atlantic coastline southward into the Florida Peninsula and Keys, across about 50 km of open ocean to northwestern Cuba, and thence southwestwards across the 200 km Yucatan Channel to the Yucatan Peninsula in Mexico. In addition to the evidence provided by a single recapture in Cuba, (Fig. 2 in Urquhart & Urquhart 1978a), Urquhart and Urquhart (1979b, 1979c) and Urquhart (1987:138–143) supported their contention by stating that (1) they had observed monarchs flying with a strong onshore wind into the Yucatan during October 1978, (2) overnight roosts had been seen in Cuba, and (3) their field assistant had made numerous observations of overnight roosting clusters in eastern Yucatan. The Urquharts held that these monarchs continue flying westwards across the Yucatan Peninsula to hypothetical overwintering sites in Guatemala or Honduras.

Possible direct evidence for a southerly migration during November 1985 along the eastern coast of the state of Quintana Roo in the Yucatan was cited in de la Maza and Calvert (1993). Deductive reasoning that supports the hypothesis is in Baker's (1978:424) analysis of Urquhart's (1960) speed of flight data which gave a maximum daytime flight distance for individual monarchs of 130 km. Assuming moderate wind assistance, the distances are short enough that hopscotching from the Florida Keys across Cuba to the Yucatan seems a viable possibility. That wind assistance is possible is supported by observations of monarchs scudding along with cold fronts at several hundred meters above the ground during the fall migration in Minnesota (Luggar 1890), during October in Arkansas (Merrill, in Williams et al. 1942:166), and on 9 October 1994 in central Texas (Brower et al. unpublished data).

Biogeographic evidence may also support this dispersal route. The lighter colored *Danaus plexippus plexippus* from North America shows clinal intergradation in southern Mexico and in Central America with the darker *Danaus plexippus megalippe* (Hübner) from northern South America. The intergradation could result from the invasion of northern monarchs westwards across the Yucatan and Guatemala, followed by interbreeding with *megalippe* (see Godman & Salvin 1879–1901, Clark 1941, Williams et al. 1942:158–159, Figs. 18A–C). However, a southward over-shooting of the Mexican overwintering sites in the fall, or dispersal southward from the overwintering sites in the spring, could have the same effect. More research is needed to resolve the issue.

Eastern Dispersal Route 2: Cross-Atlantic to Bermuda. Even though the Bermuda island group is 1040 km from Cape Hatteras, a dispersal route eastwards over the Atlantic ocean to Bermuda is supported by the older literature. Monarchs were first recorded in Bermuda in November 1847, and by 1859 were common and breeding throughout the year (Hurdis, in Jones 1859, Hurdis & Hurdis 1897, Tutt 1900:237, Verrill 1902:763). Since there were no native asclepiads in Bermuda, monarchs could not have become established prior to the introduction of *Asclepias curassavica* L. or *A. physocarpa* Schlechter (Asclepiadaceae) (Hilburn 1989, Ferguson et al. 1991).

Migrating individuals, thought to be riding eastward on cold fronts or hurricanes, arrive in Bermuda from the mainland in September and October. For example, on 4 September 1970 several thousand monarchs were reported flying in from the ocean and clustering on the imported Australian "pine," (*Casuarina equisetifolia* L. Casuarinaceae) (Ferguson et al. 1993). The arrival of other butterfly species on Bermuda support this windborne hypothesis: Jones (in Scudder 1876) had noted large numbers of *Terias lisa* (Pieridae) suddenly arriving in Bermuda in 1875 and attributed their arrival to having "been caught up by the winds in a period of great atmospheric disturbance, and whirled over the sea to this island" (p.395).

Other supporting evidence for dispersal to Bermuda was presented in Urquhart (1976a): Sabo reported from an oceanographic expedition that he had seen more than a thousand monarchs flying over the Atlantic near Bermuda during an 8 day period in September, 1973. An earlier observation at sea, associated with a hurricane, was made in September 1944 by Varey (quoted in Urquhart 1987:140–141): "we ran through a massive swarm of monarch butterflies. . . . I remember standing on deck watching this mass of colorful creatures fluttering around the ship's rigging." This encounter occurred immediately *after* the ship steamed westward through the eastern edge of the hurricane, about 1600 km east of New York. Brewer (1967:167) had earlier documented the landing of large numbers of monarchs on a Coast Guard vessel in the Atlantic Ocean in the fall of 1941; these butterflies presumably were blown out over the Atlantic Ocean by a hurricane.

The eastern dispersal route to Bermuda is thus supported by direct observations of monarchs at sea, witnessed arrivals, and the breeding populations that have been established there for well over a century. However, cross-oceanic dispersal to islands could not have been an adaptive behavior prior to the introduction of milkweeds. Thus monarchs migrating to such places as Bermuda would have died without issue unless they could return to the mainland. To date, there is no evidence for a return migration to the U.S.A. from Bermuda, Cuba, or any of the other marginal southern destinations of the dispersing fall migrants.

Eastern Dispersal Route 3. A subset of the monarchs that are blown towards Bermuda constitutes the Urquharts' third hypothetical group. The authors postulate (supported by minimal data in Urquhart & Urquhart 1978a, Fig. 2, p. 614) and Urquhart 1987:142–143) that these monarchs somehow recover a southerly orientation and pass through the Bahamas and the Antilles to Central or South America, ultimately to winter in the mountains of Guatemala, Colombia, or Venezuela.

Synthesis: (a) The Trans-Oceanic Dispersals. To accept these three trans-oceanic dispersal routes as fall migration routes requires that monarchs succeed in reaching overwintering sites and then return to the southern U.S.A. the following spring, as is now proven for the main cohort that overwinters in Mexico (Malcolm et al. 1993). The extensive tropical lowlands through which the reproductively-repressed adults would have to fly during the September-November migration period are hot. For example, mean monthly temperatures during October through December in Quintana Roo (southeastern Yucatan) exceed 23°C (Snook 1993b). Consequently, any butterflies reaching mainland Central or South America would almost certainly undergo rapid gonadal maturation (Johnson 1963), mate with the local non-migratory populations, reproduce, and die before ever reaching the hypothetical mountain overwintering sites (Brower 1985a:757). Peter Hubbel (pers. comm. 1994), an entomologist who has collected extensively in Guatemala, has never observed any clustering in the mountains, and there are no solid records of overwintering sites in any of the Urquharts' postulated Central or South American areas (de la Maza & Calvert 1993).

I therefore tentatively conclude that the Urquharts' "aberrant migration" routes over the Atlantic Ocean to hypothetical Central and South American overwintering sites are best considered as failures of the fall migration to Mexico. Rather, they, as well as the chance arrivals in Bermuda, probably constitute emigration and dispersal routes, with only a remote possibility that these individual monarchs or their offspring can ever complete a spring remigration to the northern breeding grounds in the U.S.A. or Canada.

Let me inject a caveat, however. It took more than 100 years for scientists to find the Pelon and Chincua Mexican overwintering sites that are less than 125 km from Mexico City. Rais (1964) referred to the Neovolcanic Plateau as the "the cultural-historical center of Mexico." Lack of interest in recording local natural history phenomena may well be a parsimonious explanation of our ignorance of other overwintering areas in Central America, or even elsewhere in Mexico. Thus, although the broader biological picture of the monarch argues against the existence of other overwintering sites in Central and South America, it seems worthwhile to continue looking for them.

Synthesis. (b) East of the Appalachians: what happens to the Atlantic Coastal and Florida fall migrants? Focusing on the aberrant dispersal routes ignores the importance of the monarch migration east of the Appalachians. As seen above, the historical anecdotal evidence indicated a predictable annual fall migration along the Atlantic Coast with occasional spectacular years. My colleagues and I have initiated a new program that is providing a long term data base on the fall migration through Cape May, New Jersey. We have so far recorded a regular migration through the area for four years during September and October (see Walton 1993, 1994). This research also determined that there is a high correlation between our Cape May migration data and the previous Fourth of July monarch counts taken annually east of the Appalachians during the monarch's summer breeding period (Swengel 1990, Opler & Swengel 1992). This correlation strongly argues that it is incorrect to consider the migration along the east coast of the U.S.A. as aberrant (Walton & Brower 1995).

The major clue to the fate of the migrants east of the Appalachians is the lack of recurrent literature reports of migrations southward through the Florida peninsula (see above for the frustrating searches for overwintering populations in Florida; see also Urquhart 1960, 1987:100–101, 138). I am led to conclude that the majority of monarchs breeding east of the Appalachians either migrate southwestward through these mountains, or, if they migrate along the coast to southern Georgia and Northern Florida, they turn westward and fly towards the Gulf Coast. Eventually these butterflies probably join the major southwesterly migration to Mexico. Those that get blown out over the Atlantic by westerly winds and storms have lost control of their destiny. Prior to the spread of milkweeds by humans (see below), these butterflies would have perished.

Systematic, quantitative research on the fall migrations in relation to weather patterns is clearly needed, as has been done for bird migrations (e.g., Alerstam 1990). The periodic appearance of large numbers of fall migrants on and near Nova Scotia and Newfoundland (e.g., Brown 1950, Ferguson 1955, Jackson 1974, Urquhart 1974, Maddox & Cannel 1982), where native milkweeds do not occur, probably also represent monarchs that are blown off course. It would be interesting to search old newspaper records of Atlantic coastal towns from Quebec and Newfoundland to Florida, and correlate reports of migrations with weather patterns over the years.

LONG DISTANCE DISPERSAL ACROSS THE ATLANTIC AND PACIFIC OCEANS

Nineteenth century biologists witnessed a rapid expansion of the geographic distribution of the monarch butterfly from North America across both the Atlantic and Pacific Oceans, distances of 5,000 km and more. According to Ackery and Vane-Wright (1984), the first sighting in Europe was by Llewelyn (1876). A "fine fresh specimen" (p. 108) was captured in southern Wales on 6 September 1876, which Llewelyn and the editor suggested could have been transported as a chrysalid "or even . . . a perfect insect" on one of the many ships from America sailing into the Bristol Channel. Distant (1877:94) formalized the first hypotheses to explain these long distance dispersals and island colonizations: "We are justified in considering the principal and only factors, as winds, [ocean] currents, and the agency of man. . . and whether the dispersals are. . . voluntary or involuntary migration." Distant was aware of bird migrations to England as well as many sightings of butterflies from ships at sea, and suggested that riding wind currents, landing on ships, and possibly even riding on terrestrial vegetation carried along by the Gulf Stream were ways monarchs might cross the Atlantic.

In reviewing cross-Pacific flights, Gulick (in Scudder 1875, and elaborated in Scudder 1889:730–731) noted that monarchs were found in the Sandwich (=Hawaiian) Islands after a neotropical *Asclepias* (presumably *A. curassavica*) had been introduced. Gulick moved from Hawaii to the western Pacific and recounted how he had accidentally naturalized *Asclepias* seeds in the Caroline Islands (NW of New Guinea). He reasoned that the milkweed seeds must have been in the soil accompanying a tightly packed shipment of plants that he had brought from Hawaii to introduce and cultivate. To his astonishment, monarch larvae appeared on the young milkweeds shortly thereafter (an alternative possibility is that *A. curassavica* had already become established prior to his arrival; because of its ornamental properties, this neotropical milkweed was widely disseminated through the old world tropics and Oceania, including Tahiti; Pickering 1879:983). With the details provided by Gulick, Scudder deduced that the larvae must have been the progeny of one or more monarch adults that had arrived on the same ship. Bowles (1880) bolstered Scudder's argument by documenting a monarch that had been captured on shipboard in the Atlantic hundreds of kilometers from shore. By 1886, Scudder was firmly convinced that the transoceanic dispersal of monarchs was a consequence of the serendipitous transport of adults on commercial ships.

In contrast, Walker (1886:222), in thoroughly documenting the rapid monarch colonization of the south Pacific Islands, Australia, and New Zealand, presented an alternative hypothesis: both the *A. curassavica* seeds *and* the monarch adults had been naturally transported to the islands by winds: "It is . . . not difficult to imagine one of the great migrating swarms of *Anosia plexippus* being blown out to sea from the Californian or Mexican coast, and traveling with the NE trade wind; the greater number by far perishing en route, but a few stragglers . . . would reach the . . . islands . . . I should imagine . . . the light and downy seeds of the *Asclepias* could be carried by the agency of the winds . . . alone." He viewed crossing the "much more stormy" Atlantic with its "less steady winds" as more difficult, and suggested that monarchs complete the trip by "resting . . . on the numerous vessels constantly crossing the Atlantic." Meanwhile, Webster (1902:797) had written a general review of the role of wind in dispersing insects and stated that "The influence of high winds on insects is illustrated . . . by the great number of butterflies that are sometimes encountered by ships at sea, long distances from land."

Comstock and Comstock (1904) promulgated the hypotheses that the transoceanic colonists had arrived "Either by flight or as stowaways in vessels" (p. 206). Walker (1914) subsequently concluded that natural wind dispersal across the oceans was more important than human-caused dispersal. An additional possibility raised for the trans-Pacific dispersals was the purposeful human distribution of monarchs to control the exotic asclepiads which had become troublesome weeds (Scudder & Gulick 1875, Walker 1886:219). Felt's (1928) extensive review of insect dispersal in relation to global wind patterns considered the monarch a prime candidate for dispersal across the Pacific and Atlantic Oceans by normal wind currents and storms, and minimized the importance of ships. Williams (1930) agreed with the wind dispersal hypothesis, but also cited an additional observation (in Barrett 1893) of several monarchs flying amongst the rigging of a ship 320–480 km from the British shore. Another sighting of a monarch in the Atlantic 97 km off of Portugal was made by Harker (1883), and a century later two monarchs were captured on the deck of an oceanographic vessel in the Gulf of Mexico, 800 km off the coast of Florida (Wolf et al. 1986). Ford

(1945:160) favored the hitch-hiking hypothesis, but, like Walker, was baffled by the simultaneous arrival of several monarchs in southern England in some years e.g., 38 records in 1933 (Williams et al. 1942: 181) and 12 citings in 1983 (Bretherton 1984). Urquhart (1960:192–195, 1987:145), citing an additional observation of fall migrants taking refuge on a small sailing vessel in Lake Ontario during a strong wind, also endorsed the hitch-hiking hypothesis, as did Scott (1986:230).

In my judgment, Sabo's observation (in Urquhart 1976a) of more than a thousand monarchs flying over the Atlantic near Bermuda, with some landing on the oceanographic vessel, provides the solution to this long-standing debate: wind dispersal and hitch-hiking are complementary, not competing, explanations of long distance dispersal of monarchs to the Atlantic and Pacific islands, mainland Europe and Australia (Anon. 1871, Miskin 1871, Anon. 1898, Tutt 1902:318, Owen & Smith 1989). Since monarchs easily find isolated milkweed patches (Shapiro 1981, Brower 1985a, Malcolm & Brower 1987), the successful establishment of a breeding population by the dispersed butterflies is virtually inevitable if they make a successful landfall where one or more exotic milkweed species had already become naturalized. However, the few dispersers that make it across oceans for very long distances to landfall on any of the Atlantic or Pacific Islands, Australia, New Zealand or Europe will have no possibility of a return migration to North America. I conclude that a combination of wind dispersal and hitch-hiking on ships is the most reasonable hypothesis to explain the dispersal of monarchs across the Atlantic and Pacific Oceans during the 19th century.

THE "COLUMBUS HYPOTHESIS" AND THE EVOLUTION OF MONARCH MIGRATION IN NORTH AMERICA

In distilling the ideas about the rapid transoceanic colonizations, Richard Vane-Wright of the British Museum of Natural History (1986, 1987, 1993) rejected both the hitch-hiking and wind dispersal hypotheses in favor of his novel "Columbus hypothesis." There are two major parts of this hypothesis. First, early deforestation of both northeastern and western North America are held to have resulted in a massive increase of milkweed biomass that caused monarch populations to explode in the 19th century. In effect, monarch 'shrapnel' from the explosion is held to explain the rapid transoceanic colonizations, which were essentially completed by 1880. Secondly, the current coordinated migration and overwintering cycle in North America, including the large monarch roosts in Mexico, is held to be less than 200 years old.

At least three critical assumptions lie behind Vane-Wright's Columbus hypothesis: (1) prior to clearing the American forests, the monarch had not yet evolved its current patterns of migrating and overwintering. In his words: ". . . the annual coordinated migration and massed overwintering cycle is a very recent phenomenon." (1993:179); (2) lacking a well developed southwesterly orientation, the vast numbers of individuals produced on the new milkweed supply growing in the cleared forests would, in addition to flying south, disperse in westerly or easterly directions towards the oceans, and a few would succeed in colonizing the Pacific and/or Atlantic islands; (3) flying out over the oceans would result in enormous mortality. As a consequence, strong selection over the 200 year period would have resulted in the rapid evolution of unidirectional migrations, the complex swarming and bivouacking behavior that occurs during the fall migration, and the highly organized overwintering behavior that involves dense clustering of thousands to millions of individuals, as currently occurs in California and Mexico.

Malcolm and Zalucki's (1993b) critique of the Columbus hypothesis emphasized that Vane-Wright made an additional key assumption: deforestation resulted in a net increase of milkweed biomass in the northern breeding range of the monarch. I agree with Vane-Wright that breeding monarchs probably did shift eastwards from the prairie milkweeds to take advantage of the increasingly abundant *Asclepias syriaca* that was colonizing the newly cleared northeastern forest. While a net increase in milkweed biomass probably did occur, certainly the biomass of more than 20 species of milkweeds growing naturally in the nearly half billion acres of the original prairie also must have been enormous (see above, "Did the migration expand eastwards during the latter part of the 19th century?").

A major weakness of the Columbus hypothesis is Vane-Wright's assumption that because monarch overwintering clusters in California were not reported in the early literature, the complex migration-aggregation-overwintering behavior did not evolve until late in the 19th century. This seems highly unlikely given the fact that migration and aggregation behaviors occur not only in numerous Old World danaid species in five genera (*Euploea, Tirumala, Ideopsis, Parantica,* and *Danaus* (*Salatura*) (Wang & Emmel 1990, Scheermeyer 1993), but also in *Anetia briarea* in the Dominican Republic (Ivie et al. 1990, Brower et al. 1993). The common behavioral attributes in these divergent species groups of the Danainae suggests that features of the migration-aggregation syndrome are ancient characters of the subfamily.

Lane (1993) uncovered an early report of clusters in the fall of 1873 in California, probably in Pacific Grove (Anon. 1874). This predated Bush's (in Riley & Bush 1881, 1882) observation, and is important, not for pushing back the discovery date of California overwintering, but rather because the report had been overlooked by the scientific community until 1993. I submit that the nine year hiatus between this and Bush's report indicates that 19th century residents of the Monterey region had probably long known of the overwintering phenomenon, but were so involved in their own individual pursuits (e.g., Steinbeck 1954:258–262) that they either ignored the butterfly clusters or took them for granted. Shepardson (1939:18) pondered the same question and concluded that "nothing smaller than a bear would have attracted the. . . [early settlers'] attention." Lucia Shepardson's hypothesis that residents simply ignored the phenomenon is supported by the fact that, despite the existence of numerous overwintering colonies near several University of California campuses, remarkably few research papers were published on the biology of California monarchs before 1969 (e.g., Kammer 1970).

In my judgment, the rapid rate of evolution (200 years) required by Vane-Wright's Columbus hypothesis to account for the complex of monarch behaviors involved in the current Mexican and Californian migrations is impossible. The short time is also at odds with Kitching et al's. discussion (1993) of the likelihood that the monarch's clade (i.e. the subgenus *Danaus*) evolved in South America during the Pliocene from Old World stock that had arrived in the New World at an earlier time (see also Grehan 1991). According to this hypothesis, a progenitor of *Danaus plexippus* crossed the land bridge from South to Central America that had formed towards the end of the Pliocene, about 3 million years ago (timing from Delcourt & Delcourt 1993:71). The Great Plains and prairie environment had begun expanding by this time (Graham 1993:69), so that the monarchs must have been increasingly able to extend their breeding range northward with the expanding milkweed flora (Woodson 1954). However, because of their tropical origins, the butterflies would have had to retreat southwards each fall to avoid freezing.

With the arrival of the Pleistocene, the alternating glacials and interglacials would have caused major contractions and expansions of the geographic ranges both of the Oyamel forests in Mexico and the milkweeds in northern Mexico, the United States and southern Canada. The necessity of retreating southwards each year, together with these longer term movements of the evolving flora, must have been powerful selective forces affecting the evolution of the monarch's current migration biology (see also Brower 1977a, 1986, Young 1982).

If this scenario is correct, the monarch's current migration in North America could have evolved gradually over the approximately 1.75 million years of the Pleistocene, rather than almost instantaneously as postulated by the Columbus hypothesis. As McNeil et al. (1994:13) concluded in a recent review of insect migration: "Migration is not a random act of 'casting one's fate to the winds' but rather a physiologically coordinated sequence of behaviors, determined by both genetic and environmental factors." Wind dispersal combined with hitch-hiking on ships seems a completely adequate hypothesis to explain the 19th century transoceanic colonizations. Unless compelling new evidence is forthcoming, the Columbus hypothesis seems untenable.

CAN MONARCHS MIGRATE BACK AND FORTH ACROSS THE GULF OF MEXICO?

Evidence that monarchs fly across the Gulf of Mexico is indirect and weak. For several years between 1981 and 1993 monarchs have arrived almost synchronously in late March and early April in eastern Texas, Louisiana (Lynch & Martin 1993, Riley 1993), and north central Florida (Cohen & Brower 1982, Malcolm et al. 1987, 1993, Zalucki & Brower 1993). If returning migrants follow the Gulf Coast northward and then eastward, they should arrive in Texas earlier than in Florida. The nearly simultaneous arrivals suggest, but do not prove, that a broad wave of butterflies could be crossing the open water. Indirect evidence for a fall migration over the Gulf is a report of large numbers of monarchs flying ashore near Veracruz, Mexico (de la Masa & Calvert 1993).

Recent observations of monarchs and other insects landing on oil rigs in the Gulf of Mexico have been cited as evidence of cross-Gulf migrations (Baust et al. 1981, Wolf et al. 1986, Mather 1990). More than 3,000 oil and gas production platforms have been installed in the Gulf at various distances from the Louisiana shore, and Ross and Behler (1993) and Ross (in Stutz 1993) reported monarchs landing on more than 20 platforms during March and October of 1991 and 1992. Hundreds, if not thousands, were said to have landed on at least one platform in both years. The authors interpreted their observations as indicative of a 145–160 km wide flyway from the U.S.A. Gulf Coast to Tamaulipas, Mexico, as Mather's (1990) hypothetical map had suggested.

The conclusions drawn from the oil rig observations did not consider alternatives, and reflect the speculative nature of much of the literature on transoceanic butterfly migrations (e.g., Larsen 1993). For example, the oil platforms could be serving as artificial islands that permit chance interceptions of monarchs that have flown, or have been blown, off of a land course to or from Mexico. Landing on the oil platforms is analogous to the many observations of monarchs landing on ships at sea, as discussed above.

Since the distance from the Mississippi Delta to one suggested landfall in Mexico i.e., Tampico (Mather 1990) is greater than 1,000 km, migration across the Gulf of Mexico could only be achieved if monarchs

(1) do not avoid flying over water, (2) continue flying at night, (3) rest on the ocean surface, or (4) exploit tailwinds.

Are monarchs reluctant to cross large bodies of water? In noting the great fall swarms of monarchs seen in New Jersey, Holland (1898: 82–83) stated that "The swarms pressing southward are arrested by the ocean." From observations on Long Island, New York, Shannon (1915, 1916:229) maintained that fall migrants generally followed the shore rather than heading out over open ocean. Holding to this position, he later speculated (Shannon 1954:237) about a group that had been reported 24 km at sea: "it is likely . . . that few of these venturers ever regain the land." Urquhart (1960:86) and Urquhart and Urquhart (1979c: 44) agreed with Shannon's position, stating that monarchs have an "antipathy" to flying across the Great Lakes, instead moving along the shores. In contrast, Alexander (in Moffat 1901b:48) reported sailing on Lake Erie "for hours through a flock of *Archippus*" flying southward. Teale (1954:59–61) similarly observed 64 monarchs flying southwards from Point Pelee into a headwind and across Lake Erie during the fall migration. Jackson (1974), reporting the largest number of monarchs ever seen in Newfoundland during September 1973, stated that fisherman had also seen monarchs flying past their boats while three miles out at sea.

Later, in discussing the westerly rather than the usual southwesterly heading of fall migrants along the Florida Gulf Coast, Urquhart and Urquhart (1980:722) maintained that "the change of direction from a southward to a westward movement is due to an apparent antipathy on the part of the migrants to travel over large bodies of water where distant land masses are beyond the optical range of the butterflies. . . . The occasional migrant would fly out over the water only to return again to land." Three recent studies support the Urquharts' contention that individual monarchs flying out over the Gulf of Mexico tend to turn back towards land (Schmidt-Koenig 1985, 1993, Ishii et al. 1992).

Do monarchs fly at night? Whether monarchs can fly at night is controversial. In the only published nocturnal observations of which I am aware, Jennie Brooks (1907:110) stayed up all night watching clusters of monarchs during their fall migration through Lawrence, Kansas: "The night was cloudless and absolutely without wind . . . the butterflies slept on, and on, and on, with wings tightly folded together" until the rays of the sun fell upon them the following morning, and then . . . "as if touched with a magic wand, the mighty colony . . . wafted into the air." A less poetic description of nocturnal inactivity during a large fall migration through the Blue Ridge Mountains of Central Virginia in October 1935 was reported by Walton (in Clark 1941:536): "when night came they would all rest just where darkness caught them."

These observations of total quiescence through the night are in disagreement with several other reports. Thus, in describing monarchs overwintering in California, Inkersley (1911:283) stated "During their stay in Pacific Grove the monarchs set out daily at an early hour, often before sunrise, to gather honey . . . frequently not flying homewards till some time after sundown." Likewise, in reporting a migration over Chicago on 16 September 1952, Fulton (1953) said that a few stragglers continued to pass "as late as the time of the sunset." The most dramatic evidence for nocturnal activity was that of Merrill (in Williams 1942: 166, Williams 1958:105) who reported seeing thousands of monarchs through a telescope trained on the moon in Arkansas on 21 October 1921. How he identified the butterflies as monarchs was not described.

Some authors have taken firm positions on nocturnal behavior without presenting any evidence. Thus in Shepardson's (1939:28) description of Pacific Grove, she said: "One indisputable fact is that butterflies are in no way nocturnal . . . they can not travel after dark." Park (1948) also stated that monarchs do not fly at night. Urquhart (1965a:31) claimed that caged monarchs did not fly in the dark and therefore concluded that free flight at night was "improbable." His position against nocturnal flight subsequently was elevated to fact, without additional experimentation or observations (Urquhart & Urquhart 1979c, Urquhart 1987: 142, 145, see also Moffet 1985). In his review, Johnson (1969:538) interpreted the available literature differently, and stated that monarchs "proceed alone by night as well as by day" during their northward spring migration. This, in turn, appears to have been the basis for Rankin's (1978:11) statement that there is nocturnal flight during the monarch's spring remigration.

Other authors reiterated previously-published ambiguous reports (e.g., Tutt 1900:69, Williams 1930:342) and in some accounts it is impossible to determine whether authors saw monarchs flying at night, or whether they saw monarchs roosting at night (e.g., Pribble, in Scudder 1899). It may be that monarchs flying in to aggregate on trees or other vegetation at dusk (Lugger 1890, Dernehl 1900, Shannon 1915) have been mistakenly interpreted as butterflies migrating at night. Some reports of nocturnal flight may be artifacts of monarchs being attracted to bright lights, such as lighthouses, sports arenas, and vehicle headlights, from nearby roosting clusters (e.g., Merriam, in Felt 1928:101, Heitzman 1962, Shields 1974:236). Heitzman (1962), Neck (1965), and Kendall and Glick (1972) reported monarchs and other butterflies being attracted to lighted moth traps, and suggested that these butterflies had been disturbed from their roosts by the investigators, other insects, or predators. While Ross and Behler (1993) and Ross (in Stutz 1993) reported that the monarchs landing on oil platforms in the Gulf of Mexico remained there through the night, Ross (1993:3) also wrote that "many of the offshore migrants continue to fly long after dark." A possible explanation of the latter observation is that the butterflies had settled on the oil rigs in late afternoon but became activated by bright lights on the oil rigs after dark. Kingdon's (1932) report of *Pyrameis cardui* L. (Nymphalidae) flying at midnight around a ship's light 140 km at sea may have been a similar artifact.

A final ambiguous report is of a male monarch nectaring on a flowering *Eupatorium* late at night (Neck 1976b). It is possible that this could have been a dead butterfly which had been ambushed by a predator such as a crab spider (Thomisidae), e.g., Larsen (1992).

In addition to all the conflicting reports, no one has attempted to sort out how the flight behavior of monarchs in the late afternoon is influenced by diminishing light *and* lowering ambient temperatures. Our thermoregulatory studies in Mexico (Masters et al. 1988, Calvert & Brower 1992) indicate that sudden shadowing by a cloud can cause monarch body temperatures to fall below flight threshold, even in flying butterflies. This raises the possibility that migrating butterflies may be forced to land early on days when they are overtaken by a cold front. What happens to the migrating butterflies as night approaches if the ambient temperature remains high or suddenly shifts upwards remains moot. Moreover, does moonlight play any role? While the evidence summarized above is clearly inconclusive, I believe that long distance powered flight by monarchs at night is unlikely. However, it remains possible that they may be able to continue to fly on warm nights during favorable weather conditions.

Is resting on the ocean surface possible? If monarchs cannot fly at night, flight across the Gulf of Mexico could still be possible if the butterflies alighted on the ocean surface for the night and flew off again the next morning. Although this behavior was suggested by Williams (1930:342), most evidence indicates that landing on water for more than a few minutes is lethal. Monarchs do seem able to land on the water surface for short periods of time. Sabo (in Urquhart 1976a) observed monarchs alighting on the ocean surface for about 20 seconds and then flying off again. Seitz (1909:77) had noted similar behavior: "I very often saw *plexippus* at sea flying at a very considerable height, and observed that it could settle on the surface of the water with the wings expanded and rise again without difficulty into the air."

Tutt (1900:257) argued that butterflies, including monarchs, landing on the ocean surface would become waterlogged rapidly, particularly if they repeatedly landed and flew off. One of Urquhart's (1965a) experiments supported this conclusion: monarchs downed on the surface of water became waterlogged and incapable of flying off again after about 20 minutes. Another hazard of flying across large bodies of water was noted off the coast of Jamaica during one of Christopher Columbus' voyages: huge numbers of butterflies were said to have perished as a result of a heavy rainstorm (Riley 1880a).

Numerous reports made during the fall migrations indicate that monarchs are at risk of becoming trapped in water. Rogers (1872), Bowles (1880), Moffat (1901b:48), Beall (1946), Teale (1956:59) and Brown (1992) reported dead or dying monarchs beached along the shores of the Great Lakes, and Webster (1914) reported similar fall mortality along the Atlantic Coast in South Carolina. During the spring remigration in April 1906, Jones (in Clark 1941:535) noted many dead monarchs "washed up by the waves" along the shore in Virginia Beach. William Beebe (in Hutchings 1923) was reported to have observed millions of monarchs drowned at sea. Mortality during the spring was also observed along the Gulf Coast at Padre Island, Texas on 26 March 1962 by Heitzman (1962). The chain of events leading to the presumed drowning of these butterflies is unknown. Possible causes of landing on the water surface include: (1) exhaustion due to running out of lipid energy reserves; (2) being overtaken by advancing darkness; (3) being cooled below flight threshold by advancing cold temperatures; or (4) being pelted out of the sky by heavy rain.

The combined evidence thus supports the hypothesis that migrating or dispersing monarchs can land on water for short periods of time, but it is highly unlikely that they could rest there for more than a few minutes, and virtually certain that they could not spend the night resting on any body of water, including the Great Lakes, the Gulf of Mexico, or the Atlantic or Pacific Oceans.

Monarchs may fly across the Gulf of Mexico on strong tailwinds. Winds across the Gulf of Mexico apparently do blow predominantly southward in the fall and northward in the spring (Rankin & Singer 1984, 1986, Wolf et al. 1986). Strong fronts, combined with powered and soaring flight, could conceivably increase the monarchs' flight speed sufficiently to make the 1,000 km crossing during a single day (Gibo & Pallet 1979, Gibo 1981, 1986, Buskirk 1980, Drake 1985).

Synthesis. The inconclusive nature of the evidence pertaining to each question raised in this section is, to say the least, frustrating: we lack sufficient critical data to determine if monarchs regularly fly across the Gulf, or whether they fly at night, land and survive on the water surface, or use tailwinds for rapid long distance migration. My own assessment of the historical data base is that monarchs are reluctant to fly out over large bodies of water when an alternative land route is possible; that they probably cannot utilize powered flight at night; that they probably cannot survive for more than a few minutes on any water surface; but that they may be able to migrate across the Gulf of Mexico by exploiting strong tailwinds during the daytime, and perhaps also at night. It seems worth emphasizing that the elaborate aggregation ("swarming") behavior that occurs at dusk as monarchs settle on trees and bushes along the fall migration routes is consistent with the hypothesis that normal monarch migration evolved as a means of flying over land during daylight hours. Novel quantitative methods need to be devised to solve these problems. Current radar technology that can indicate the size and altitude of individual migrating insects (e.g., Reynolds 1988) may provide a key to exploring the extent to which monarchs cross the Gulf of Mexico.

Is There an Intermingling of the Eastern and Western Populations?

Substantive evidence on the degree to which eastern and western populations intermingle along their Rocky Mountain interface is lacking (Malcolm & Zalucki 1993b). Williams' review maps and tentative conclusions (Williams 1938, 1958, Williams et al. 1942) suggested that the two populations are almost completely isolated. While the Urquharts have never provided convincing data bearing on the issue, they have for years stated that there is substantial interchange between the two populations (Urquhart 1966a, 1987, Urquhart & Urquhart 1977a). Most recently, Urquhart (1995:6) summarized his position as follows: "There is definitely gene-flow in the north in the area of the Snake River and in the south along the Gulf Coast to Mexico ensuring a uniform physiological species" i.e., throughout North America. Currently available distribution records shed little light on the question (e.g. Ferris & Brown 1981:407).

A recent study attempted to address this issue by analyzing the extent of mitochondrial DNA divergence between two samples of 12 monarch adults collected from eastern and western overwintering populations (Brower & Boyce 1991). The authors found virtually no differences between the two and argued that a population bottleneck probably occurred prior to the differentiation of the eastern and western migrations. Thus, the mitochondrial DNA data do not appear able to address the degree to which interchange may be occurring currently, and the question remains moot. Allozyme comparisons of individuals collected from the eastern and western populations might show differences, but have not been done to date.

Is the Eastern Population Genetically Homogeneous?

Is the eastern population of the monarch genetically homogeneous, or are there distinct subpopulations? Shannon (1916), drawing parallels between monarch and bird migration, speculated that the butterfly has four major autumn flyways: an Atlantic coast flyway, two midwestern Great Lakes flyways, and a western central states flyway (see also Williams 1938, Fig. 1, Teale 1956:90). Our 1991–1994 data indicated regular fall migrations along the Atlantic Coast at Cape May, New Jersey that strongly correlated with the previous Fourth of July summer breeding censuses in the northern Appalachian region. The correlation is consistent with the idea of a separate Atlantic flyway. Further data are needed to define the purported separate flyways west of the Appalachians, as well as the degree to which the migrations along the different flyways may or may not be synchronized (Beall 1951).

If the routes of distinct flyways led to geographically distinct overwintering areas, then we might expect genetic differentiation to occur. Based on recaptures of a few tagged monarchs in Mexico, Urquhart and Urquhart (1978b, 1980, see Urquhart 1987) proposed that subgroups of the eastern population do overwinter in geographically separated mountain enclaves in Mexico, with the implication that they return to their respective breeding areas the following spring. Thus the Urquharts proposed a sorting of monarchs with the western, central, and eastern overwintering sites representing concentrations from the Great Plains to more easterly populations.

Too few tagged butterflies have been recovered to support or reject the hypothesis (Urquhart & Urquhart 1978b, 1978c, 1979a, 1979c, Urquhart 1987:160–161), and several facts strongly challenge it. First, the geography of the overwintering sites makes such sorting unlikely: the five major sites (Chincua to Pelon) are within 30 km of each other and occur in a north to south orientation rather than the east to west orientation depicted by the Urquharts (compare Urquhart's 1987 figure on p. 160 with Fig. 1 in Calvert & Brower 1986). It therefore seems likely that butterflies from the different regions mix before and during their arrival at the different overwintering sites. Second, when the monarchs reach the overwintering sites at the end of November and in early December, most are in reproductive diapause: only 19% of 353 females from the Sierra Chincua contained one or more spermatophores during January–February 1978. In contrast, by 1 April 1978, the time of the spring remigration, 62% of the females had spermatophores (Brower 1985a, Table 1, Herman et al. 1989). Thus any potential differentiation within the fall flyways would be canceled out as the mostly virginal male and female monarchs from the entire northern breeding range intermingle over at least a two month period before mating and leaving (see also Van Hook 1993). These facts argue that the monarchs become an effectively panmictic population at the overwintering sites.

Genetic evidence derived from summer breeding and fall migratory populations supports this genetic mixing scenario. Eanes and Koehn (1978) and Eanes (1979) found that differentiation developed at several electrophoretic loci in local samples collected over the summer, but the differences were homogenized in samples from the fall migratory populations collected in the U.S.A. Even further mixing must occur as the butterflies funnel through Texas, migrate southwards along the Sierra Madre mountains, and thence westwards into the overwintering sites (Brower 1985a).

Finally (and this Eanes and Koehn did not know at the time of their study), monarchs largely recolonize the U.S.A. and Canada by the successive brood strategy shown in Fig. 1B (Malcolm et al. 1993). Following spring breeding in the Gulf Coastal states, butterflies of the new generation move northward to the central and northeastern United States and southern Canada and multiple overlapping generations are produced over the summer (Cockrell et al. 1993). Thus, the annual reproductive cycle of the monarch seems perfectly suited to explain Eanes and Koehn's summer genetic differentiation, followed by effective panmixis during the fall migration, the overwintering period and the spring remigration. Clark's (1941:534) evidence that the color pattern of the monarch "is extraordinarily constant throughout its enormous range" is consistent with this mixing hypothesis.

In conclusion, the combined evidence argues for a general lack of genetic differentiation of monarchs of the eastern population. Electrophoretic comparisons of samples from the various Mexican overwintering colonies should definitively resolve this question.

IMPLICATIONS OF THE SALINE VALLEY OVERWINTERING POPULATION IN CALIFORNIA

One mystery of the western population is the occurrence of overwintering colonies in the Saline Valley, an interior drainage basin immediately west of Death Valley in California. These were first reported by Giuliani (1977–1984). In November 1986, I visited several of these sites with John Lane in an adventure yet to be told. Recent data indicating the annual recurrence of these colonies are in Cherubini (1993) and Sakai (1994).

Overwintering in this environmentally hostile desert area that is nearly 320 km inland from the coast of California raises the possibility that other unknown overwintering sites of the western monarch population may exist in the western U.S.A. or in western Mexico, perhaps in the Sierra Tarahumara or in the Sierra Madre Occidental. A tantalizing but incomplete description of monarchs possibly migrating through this latter region (near Culiacan in the state of Sinaloa) was given by Gluecker (in Urquhart 1960:262).

MONARCH MIGRATION: AN ENDANGERED BIOLOGICAL PHENOMENON

Because the winter aggregations in California and Mexico concentrate virtually the entire breeding stock of monarchs in a few vulnerable locations, various authors have regrettably concluded that the monarch's migration in North America is an endangered biological phenomenon (Brower & Pyle 1980, Wells et al. 1983:xxi, Pyle 1983, 1983b, 1983c, Brower & Malcolm 1989, 1991).

While most of the California overwintering sites are threatened by real estate development, several are protected within state, county and town parks (Nagano & Lane 1985, Vaccaro 1992). The numbers of monarchs overwintering in California during the 1994–1995 season appeared to be the lowest ever recorded, and may be an ominous sign (Sakai 1995). The reasons for this decline are unknown, but one possibile explanation is a protozooan disease (McLaughlin & Myers 1970) introduced into the western population by experimental transfers of monarchs from the eastern population. Brower et al. (1995) reviewed the history of these interchanges and presented a series of reasons why transfers between different monarch butterfly populations should cease. A long term strategy is needed to conserve the existing California overwintering sites, as well as to restore some of the historical ones, as is being attempted in Pacific Grove (Vaccaro 1994).

In contrast to the partially protected western population, the eastern population that overwinters in Mexico is in dire straits (Brower & Malcolm 1989, 1991). The butterfly assemblages are largely restricted to the Oyamel fir forests on four mountain ranges in the Transverse Neovolcanic Belt, with the result that virtually the entire gene pool of the eastern population is dependent upon the integrity of these remaining forests. As discussed above, this frighteningly small area—800 square km—is undergoing rapid degradation due to legal and illegal wood harvesting. Such rapidly increasing forest exploitation portends International cooperation between Canada, the United States and Mexico in protecting the milkweed breeding habitats, the wild nectar sources along the migration routes as well as the overwintering sites in Mexico is a *sine qua non*.

I consider that the economic benefits that could be realized from the long term preservation of the overwintering areas would far exceed the short term income gained by cutting them down. One clear benefit is the maintenance of high quality watersheds upon which all the surrounding villages depend (Leopold 1950, 1959, Loock 1950:55). A second is the potential for lucrative tourism that is beginning to be realized at the "Rosario" site in the Sierra Campanario (de Castilla 1993, Howell & Marriott 1994). A third is the restoration of the original wildlife to the area (Leopold 1950), which in turn might contribute to tourism income over a longer portion of the year.

While allocating resources to humans versus wildlife is a contentious problem in implementing conservation everywhere, if protection of the few relatively intact montane islands of fir forests, comparable to the level of protection provided by the U.S. National Park systems, is not instigated within this decade, the eastern migratory population of the monarch butterfly will not survive long into the next century. Monarchs overwintering in Mexico are a treasure comparable to the finest works of art that our collective world culture has produced over the past 4,000 years. If we do not succeed in conserving their overwintering grounds, the eastern populations of the monarch butterfly will soon become a remnant of history, and humanity will be deprived of one of the most magnificent natural spectacles on our planet.

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In writing this review, I became fascinated by the often overlooked findings of early workers. Charles Valentine Riley's contributions to monarch butterfly biology have been largely forgotten, yet he was one of the great insect biologists who established a strong foundation for most subsequent research on the monarch. John Alston Moffat was a master at deduction, and a more careful notice of his 1902b paper might have compelled an earlier search for overwintering monarchs in Mexico. Jennie Brooks' (1911) insight that monarchs must migrate to Mexico was never acknowledged, nor was her all night watch of clustering monarchs in Kansas (1907), demonstrating that the butterflies were inactive at night. Likewise, Lucia Shepardson's two pamphlets (1914, 1939) on the monarchs of Monterey are biology classics that have been largely ignored. A recent researcher whose contributions should not be lost simply because of his iconoclastic approach is Adrian Wenner. His conclusion (Wenner & Harris 1993) that the fall migration in California lacks adequate documentation is correct. Uncritical acceptance of the fall migration of the western monarch population has a historical counterpart: just as overwintering of the eastern population was assumed to occur regularly along the Gulf Coast by analogy with the undisputed overwintering aggregations in California, so the existence of a definite fall migration in the West has been assumed through analogy with the undisputed fall migration of the eastern population.

It was difficult to complete this review because of the many recondite references in the literature. I apologize to those whose works I may have missed. I also implore those who publish their findings in any format—from letters, to the electronic media—to document each observation with localities that can be found in atlases, dates that include the year, weather conditions, and estimates of the speed and direction from which the wind is blowing, the direction in which the monarchs are flying, their altitude, and the numbers of monarchs seen per person per unit time. Many anecdotes in the literature might have better fit into the puzzle had they contained greater detail and had they been carried out in a more organized manner.

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